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Malacological Review, 1975, 8: 1-6

THE LIMPET *ANCYLUS FLUVIATILIS* IN LAKES OF THE GUDENÅ RIVER SYSTEM, DENMARK

H. N. Garner

ABSTRACT

The distribution of *Ancylus fluviatilis* in lakes of the Gudenå River system has been investigated since 1969, and this species has been found on wave-swept shores of 9 lakes. In some of these lakes, pollution seems to be a possible menace to the small populations. In addition to field observations, *A. fluviatilis* has been observed under rather adverse conditions in small standing-water aquaria, and although this species generally is found only in flowing waters, the aquaria specimens survived for as long as 164 days. In spite of this tolerance to quiet water, the habits and demands of *A. fluviatilis* in nature seem to make its dispersal to lakes slow and complicated; it has not yet occupied all suitable biotopes of the lakes of the Gudenå River system.

INTRODUCTION

The freshwater limpet *Ancylus fluviatilis* O. F. Müller, as its name implies, is found mainly in rapidly flowing brooks and rivers--with stony bottoms. However, it is commonly known that the species occasionally and rather exceptionally occurs in lakes.

Ancylus fluviatilis is distributed throughout the greater part of Europe (except the most northern parts), the Trans-Caucasus region and North Africa.

During the Boreal age the cold Yoldia Sea which filled the Baltic basin was transformed into a freshwater lake by the withdrawal of the great glaciers and the following elevation of the land. The lake thus formed had an influence on the fauna of the area, an influence which possibly may still be perceptible (Spärck, 1950: 21). This huge lake, the surface of which was higher than the current level of the Baltic Sea, has left subfossil sediments. *Ancylus fluviatilis* lived in this prehistoric lake, and the presence of *Ancylus* shells in its sediments has resulted in the lake being named Ancylussøen or Lake Ancylus.

Lake Ancylus existed during the period 7500-5500 B.C., but subsequently new geological depressions allowed sea water to enter the Baltic basin, which transformed Lake Ancylus into the saline Littorina Sea, causing *Ancylus fluviatilis* to disappear. Subfossil shells have not been found from the later periods (the Sub-Boreal and the Sub-Atlantic ages), and since the present distribution of *Ancylus* in Sweden does not follow the old shores of Lake Ancylus, the present populations in Sweden are presumed to have immigrated from the southwest (Hubendick, 1949: 55, 93).

Kaiser (1950: 69-72) discussed the observations known to that time of *Ancylus fluviatilis* in Danish lakes and explained the particular environmental demands of the species. In lake biotypes these demands seem to be the presence of a surf shore with a stony bottom, preferably with tolerably clean stones that are large and heavy enough so as not to roll with heavy wave action. Kaiser (*op. cit.*) showed that previous statements that *Ancylus* prefers calcareous water are not valid for all localities in Denmark. In 1950 *A. fluviatilis* was known from 5 Danish lakes:

Tystrup-Bavelse Sø[1] (last found in 1879 by A. C. Johansen); Rørbaek Sø (1949 by Carlo F. Jensen; 1950 by Kaiser and K. Berg); Kulsø (1950 by Kaiser); Knudsø and Silkeborg Langsø (1923 by Isager & Nielsen; 1950 by Kaiser).

In Sweden *Ancylus fluviatilis* is known from 9 lakes, amongst them Vättern and 3 lakes of Scania (Skåne): Ringsjön, Börringesjön and Rabelövsjön. The distribution of the species in Sweden reaches 61°N (Hubendick, 1949: 55). In Norway *A. fluviatilis* was, at least until 1972, not yet known from lakes, but the species has been found in rivers of the area between Lake Mjøsa and Vestfold and in the landscape of Jaeren (Økland, 1964: 142, 198; 1969: 148; pers. comm., 1973). Immediately south of the German-Danish border, *Ancylus* is found in Sankelmark Sø (Mandahl-Barth, 1949: 112), and it is known from northern Italian lakes, from the lakes Starnbergersee and Chiemsee in Switzerland and from Lake Pulvermaare in Eiffel, Germany (Berg, 1952: 264).

DISTRIBUTION IN THE LAKES OF THE GUDENÅ RIVER SYSTEM

The Gudenå is the major river of Denmark. It measures 160 km from its springs in the heart of the Jutland Peninsula to its mouth in the Kattegat. The river receives many tributaries, and its central part passes through the Danish lake district, which has about 50 small to large lakes. *Ancylus fluviatilis* is very common in parts of the Gudenå River and several of its tributaries, e.g., Salten Å, the Knudå system, Millingbaek and Voel Baek.

Since Kaiser's investigations were published in 1950, I have occasionally surveyed the 2 known habitats of *Ancylus fluviatilis* in Knudsø and Silkeborg Langsø lakes and searched for the species at other suitable biotopes in the lakes of the Gudenå River system. During this collecting, I have found only a few specimens at each biotope, and I have mostly determined only the existence of the species, as it seems to be numerous nowhere in these lakes. As a result of my investigations, *A. fluviatilis* was found in 7 lakes and at a new habitat in Lake Knudsø (Fig. 1). This information is presented below.

Mossø. In spite of a thorough investigation, I have so far succeeded in finding only a single locality for *Ancylus*, by the Hem Odde Peninsula at the southern lake shore. But as this lake has other stony surf shores, it is not impossible that the species may be found elsewhere. Lake Mossø is the 3rd largest lake in Denmark, with a circumference of about 30 km. *A. fluviatilis* was found for the 1st time in Mossø on November 29, 1969, and was found again on December 27, 1971. At the locality where the limpet was found, the wind produces one of the strongest surfs of the Gudenå lakes. The bottom here is covered with rather small, clean stones. This population of *Ancylus* is very small.

Salten Langsø. *Ancylus* was found on January 20, 1973, at the northern shore near the middle of this lake. At the locality there are a few square metres where the waves wash over a bottom of smaller, not totally clean stones. The shells of the limpets were covered with algae. The population of *A. fluviatilis* here is very small.

Gudensø. *Ancylus fluviatilis* was observed for the 1st time in Lake Gudensø on November 11, 1969, and then again in 1971 and 1973, and most recently on September 15, 1974. The locality where the limpets were found is covered with hand-sized stones which are washed with waves. The population here is rather small.

Ravnsø. On November 25, 1972, *Ancylus fluviatilis* was found near Bensmøllevad bridge, some in the stream Knudå on *Unio* shells, and some in Lake Ravnsø on

[1]Danish words: Sø = lake, Å = river, Baek = brook; Swedish words: Sjö = lake.

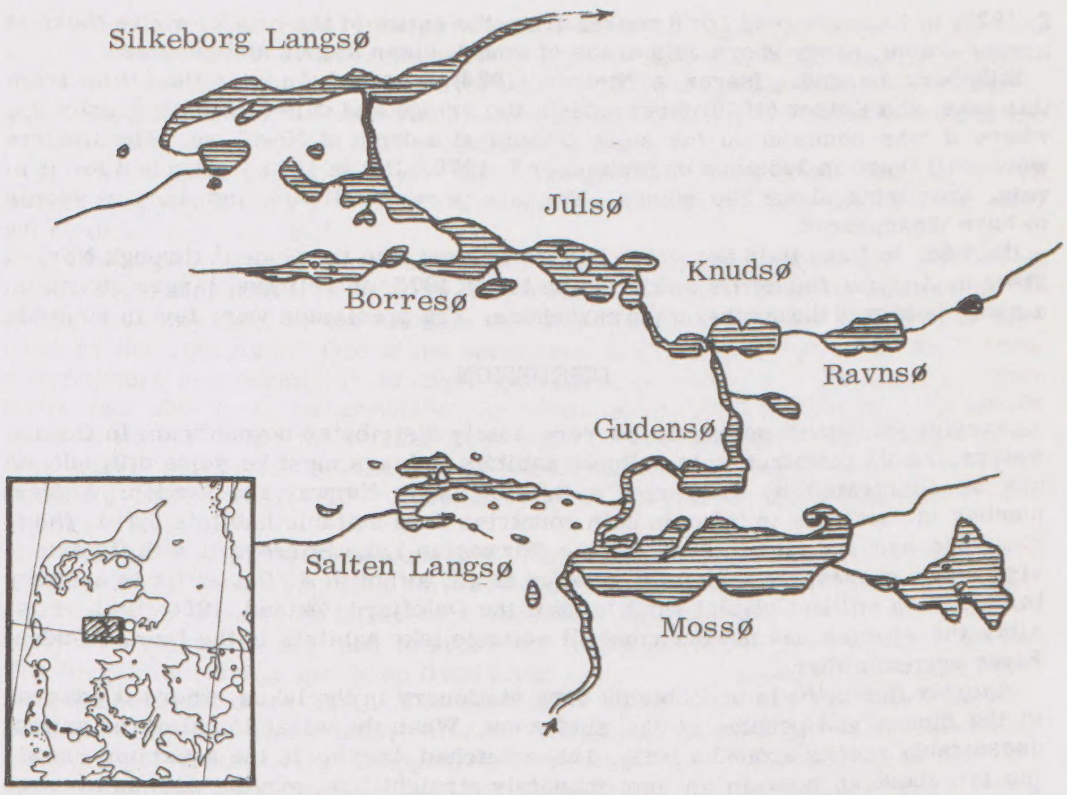

FIG. 1. Lakes of the middle stream of the Gudenå River system. Lakes where *Ancylus fluviatilis* have been found are named on the map. Lake Hald Sø is outside the map in a northwest direction.

solitary, clean and rather large stones at the western lake shore only a few metres from the effluent of the lake (the stream Knudå). The lake shore here is sandy, without bottom vegetation, and is exposed to waves brought by eastern winds. Only a few specimens of *Ancylus* were observed in the lake, but in the stream they are very common.

Knudsø. The habitat on the southern shore of Lake Knudsø, where Kaiser (1950) found 4 specimens of *Ancylus fluviatilis*, was surveyed twice in 1956 and again on September 18, 1971. The limpets were still there, but very scarce. On November 14, 1971, I found a 2nd locality, not far from the 1st one, where a brook has its outlet into the lake. At this place a number of *Ancylus* were observed behind a narrow edge of vegetation (*Phragmites*) in a small area with a stony bottom and a surf. In the brook there are no limpets.

Julsø. In this lake, *Ancylus fluviatilis* was found at the eastern shore. The bottom here is partly covered with small stones and is exposed to a heavy surf brought by western winds. The limpets were found here for the 1st time on November 25, 1965, and were observed again in 1971, and most recently on August 6, 1973, when they were relatively numerous.

Borresø. The very clear and clean small Lake Slåensø (with no populations of *Ancylus*) has its outlet into Lake Borresø through the Millingbaek. In this stony brook *A. fluviatilis* is common, but not numerous. One specimen was found on February

2, 1973, in Lake Borresø 7 or 8 metres from the outlet of the brook, where there is a wave-swept, sandy shore with areas of small, clean stones and pebbles.

Silkeborg Langsø. Isager & Nielsen (1923) reported *Ancylus fluviatilis* from this lake, and Kaiser (1950) observed it by the bridge and dam at Kaersgårdsbroen, where it was common on the stony bottom at a depth of 30-40 cm. The limpets were still there in 1958 and on September 7, 1970. But in 1971 I searched for it in vain, examining about 200 stones. The lake is very polluted, and *Ancylus* seems to have disappeared.

Hald Sø. In Lake Hald Sø, which has its effluent into the Gudenå through Nørreå Stream, *Ancylus fluviatilis* was found on July 9, 1973, on solitary, larger stones on a sandy bottom of the northeastern surf shore. The specimens were few in number.

DISCUSSION

Ancylus fluviatilis seems to be very easily distributed downstream in flowing waters, but its distribution to suitable habitats in lakes must be more difficult, as can be illustrated by the limpet's distribution in Norway and Sweden. A great number of localities in lakes in both countries have suitable habitats for *A. fluviatilis* but are not yet occupied. In the Norwegian Lake Borrevann with its extensive stony shores, there is no population at all, although *A. fluviatilis* is common in the lake's effluent rivulet which leads to the Oslofjord (Økland, 1964: 198). Possibly the species has not occupied all suitable lake habitats in the Danish Gudenå River system either.

Ancylus fluviatilis is undoubtedly very stationary in the lakes, where it adheres to the stones and pebbles of the surf zone. When the water is calm, the animal presumably creeps around a little. I have watched *Ancylus* in the aquarium crawling for about an hour in an approximately straight line, moving with an average speed of 10 mm per minute. The cap-shaped shell (Fig. 2) is rather large in proportion to the animal itself, and it must give *Ancylus* excellent protection. When the limpet is crawling, it stretches its tentacles forward, so that they just reach out under the edge of the shell. The whole edge of the shell can rest securely on the substratum, but during movement the front of the shell is raised a little, so that a narrow split is open for the tentacles.

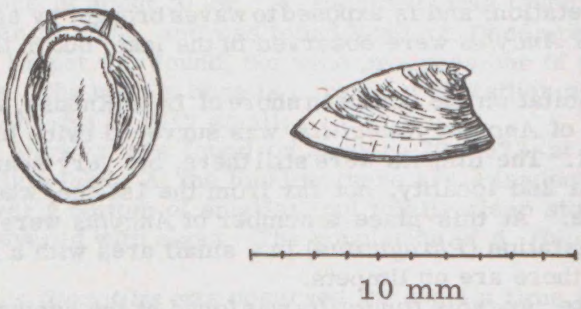

FIG. 2. *Ancylus fluviatilis* from Lake Gudensø.

If an *Ancylus fluviatilis* gets turned on its back, normally it is not able to right itself, since its foot is unable to reach over the shell to the substratum. Outside the water an *Ancylus* soon will perish by drying (Hubendick, 1949: 54, gives another point of view). However, in experiments subjecting the species to adverse aquatic conditions, *A. fluviatilis* was able to survive for long periods (see below); whether

they come from standing or flowing water, there seems to be no difference in survival of specimens. On several occasions I have kept *fluviatilis* in small aquaria in standing water, and the animals survived for months. Because of the absence of laboratory equipment, the observations were not accompanied by hydrographic investigations.

Below are listed 3 main series of observations:

1. Three specimens from Lake Salten Langsø were kept in 200-300 cm^3 of well water at a temperature of 16-20 C. The specimens survived for 30 days, after which they were removed.

2. Two specimens of *Ancylus fluviatilis* from Millingbaek Brook survived for 40 and 60 days, respectively, in 200 cm^3 of stagnant well water at a temperature of 14-20°C. The only food for the animals was algae, grown under the influence of daylight in the aquarium. One of the specimens had broken a part of the shell edge; this fracture regenerated in 40 days. Another observation was that *Ancylus fluviatilis* was able to move around on the bottom of the surface film, hanging upside down by its foot under the surface of the water, a practice often observed for other freshwater pulmonate snails. This behaviour has not been observed in nature (Mandahl-Barth, 1949: 110; Hubendick, 1949: 54; Sharp, 1883: 218, referring to Moquin-Tandon).

3. Three specimens of *Ancylus* from Lyngbygård Å (a stream outside the Gudenå River system) were kept in 300 cm^3 of standing well water. The animals fed on algae, which grew under the influence of daylight in the aquarium. A clean bit of *Unio* shell was placed in the tank to supply the animals with calcium for their shells. The longest surviving specimen lived from March 10 to August 21, 1964 (164 days) at a temperature of 10-22°C. The most amazing fact was that the Ancylidae succeeded in breeding under these extreme conditions. On June 14, 1974, 6 juveniles measuring 1-2 mm in length appeared in the aquarium. Three of these survived until September, and the last one died on September 9; their shells measured 2, 2 and 3 mm in length. Although the aquarium-maintained juveniles were growing initially, they later became emaciated. This raises the question as to whether or not there is any relationship between the reduction of the soft parts of the animal and the presumed deficiency of oxygen in that small mass of standing water. Berg (1952: 246, fig. 8c) has shown that the oxygen consumption of *A. fluviatilis* increases with increasing body weight.

The relatively strict demands of *Ancylus fluviatilis* regarding its choice of habitats in lakes and its poor ability for moving about undoubtedly complicates its possibilities for even passive dispersal. It is difficult to imagine waterbirds, fishes, etc., as vectors of any importance in the limpet's dispersion, since the animal attaches so strongly to the substrate, an attachment so strong that the shell is easily broken when trying to dislodge the limpets while collecting. It is similarly difficult to imagine the egg capsules being effective in passive dispersal (Bondesen, 1949: 184).

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Malacological Review, 1975, 8: 7-30

MICHIGAN PHYSIDAE, WITH SYSTEMATIC NOTES ON PHYSELLA AND PHYSODON (BASOMMATOPHORA: PULMONATA)

George A. Te

ABSTRACT

Michigan Physidae are here considered to comprise 5 species, 1 geographic subspecies and 8 "ecological subspecies". Extensive taxonomic treatment, mostly in table format, is given for each of the taxa. This includes re-evaluation of species synonyms, annotations on misidentifications of species in early molluscan surveys of Michigan, redelineation of geographic distribution, new shell and anatomical observations, and notes on species relationships. The systematic status of the names "*Physella*" and "*Physodon*" are discussed in detail as well as the implications of anatomical data on the higher taxonomic groupings in the Physidae. The historical background of systematics in the family Physidae is reviewed, and a detailed key to the Michigan Physidae is also provided.

INTRODUCTION

The author is currently working on the systematics of the family Physidae. The 1st part of the study, which deals with species delineation, has been completed; these delineations are based on type specimens, continuity and discontinuity of shell series, and anatomical and ecological information, where known. In my opinion, the Physidae comprise 82 conchologically recognizable entities. Forty-six of these are assigned species status; the rest are considered as either geographical subspecies or ecological subspecies. Many of the 46 species taxa are grouped under blocks of species-complexes, thereby reducing considerably the number of "discrete" taxa. With the above stated taxonomic background in hand, the Michigan Physidae have been re-evaluated in this paper.

There have been a number of previous molluscan surveys and published catalogs for Michigan. Most of these are now either wholly or partly outdated, due to changes in taxonomy. Only 29 of these past surveys contain Physidae, and these are listed in Table 1. Altogether, 34 specific and subspecific names of Physidae have been used in the state at one time or another (Table 2). Needless to say, many of these names are the result of misidentifications or unnecessary splitting of taxa. On p 14 are listed the species and ecological subspecies of Michigan Physidae that I consider valid. Synonyms which I have determined independently are listed on p 9, 11. In many cases the species placed into synonymy agree with opinions of past workers.

Table 3 lists some of the biological (i.e., non-taxonomic) studies relevant to Michigan Physidae. Nevertheless, very little is yet known about the biology of each of the individual Michigan species and "ecological subspecies", and more critical biological studies are needed. An outline of the main differences in the gross morphology of the penial complex is given on p 16-17. Additional anatomical studies are currently underway. Species relationships, as presently understood, and systematic notes on *Physella* and *Physodon* are provided on p 13, 20. And finally, conchological keys to Michigan Physidae are given on p 21-23.

TABLE 1. Surveys and catalogs of Michigan Mollusca in which Physidae have been cited.

1839	Sager	Michigan
1859	Currier	Grand River Valley, Mich.
1861	Miles	Michigan
1865	Currier	Grand Rapids, Mich.
1868	Currier	Michigan
1876	Walker & Beecher (also see Goodrich, 1943)	Ann Arbor, Mich.
1879	Walker	Michigan
1881	DeCamp	Michigan
1892	Walker	Michigan
1894a	Walker	Saginaw Valley, Mich.
1894b	Walker	Michigan
1894	Reighard	Lake St. Clair, Mich.
1896	Walker	Charlevoix, Mich.
1904	Ruthven	Ontonagon Co., Mich.
1906	Baker, F.C.	Alpena Co., Mich.
1908	Walker	Isle Royale, Mich.
1911	Baker, H.B.	Saginaw Bay, Mich.
1911	Walker	Michigan
1914	Baker, F.C.	Cass and Van Buren Cos., Mich.
1915	Walker	Charity Island, Lake Huron, Mich.
1917	Winslow	Northern Michigan
1921	Winslow	Alcona, Oscoda and Crawford Cos., Mich.
1922	Baker, H.B.	Dickinson Co., Mich.
1926	Winslow	Michigan
1926	Clench	Au Sable River, Mich.
1927	Baker, F.C.	White Lake, Oakland Co., Mich.
1931	Goodrich	Keweenaw Co., Mich.
1932	Goodrich	Michigan
1939	Goodrich & van der Schalie	Upper Peninsula of Michigan

SPECIES OF PHYSIDAE OCCURRING IN MICHIGAN

Michigan has 14 conchologically recognizable entities (Table 4), representing 5 species, 1 geographic subspecies and 8 "ecological subspecies". The distinction of geographic subspecies and ecological subspecies follows Mayr (1970, Chapt. 12: i.e., microgeographic race). The number of taxa recognized here (excluding ecological subspecies) compares favorably with 2 excellent recent regional studies: Clarke, 1973 (Canadian Interior Basin: 6 taxa) and Harman & Berg, 1971 (central New York state: 7 taxa).

A total of 3,888 museum shell lots are involved in this study. Museum lots studied are those relevant to Michigan Physidae lodged at the Museum of Zoology, The University of Michigan (UMMZ). Each lot has been critically examined and reidentified through comparison to type specimens. Table 4 shows the sample size and related information for each taxon.

BRIEF HISTORY AND NOMENCLATURE

A series of mid- to late 19th Century molluscan monographs summarized the total number of described species of Physidae known at that time. The works of Haldeman (1842), Binney (1865), Tryon (1865, 1870), Strebel (1873), Sowerby (1874), Fischer & Crosse (1877), Kobelt (1879, 1881), Clessin (1886), Paetel (1889) and von Martens (1898) are remarkable in their extensive coverage. Crandall (1901) did the first taxonomic re-evaluation of North American Physidae. Walker (1918) again summarized the taxonomy of North American Physidae. The re-evaluation of species reached a high point in the 1920's and 1930's with the works of F. C. Baker, J. Henderson and W. J. Clench. Wurtz in 1949 did the last major taxonomic study of a species of Physidae: *"P. heterostropha"*.

The first anatomical study of Physidae apparently was that of Moquin-Tandon (1855). The use of anatomy for distinguishing closely related species and in determining higher taxonomic groupings was, however, first begun by F. C. Baker (1897, 1901, 1926, 1928). A number of other studies further extended our knowledge of the anatomy of the family Physidae: Slugocka (1913), Hurst (1927), Bargmann (1929), H. B. Baker (1930), Germain (1931), Jones (1938), Mahoney (1940), Hubendick (1947), Ranson & Cherbonnier (1951), Duncan (1958, 1960), Demian (1962), Harry & Hubendick (1964), Richards (1964), Starobogatov (1967), Aboul-Ela & Beddiny (1969), Clampitt (1970), Hamilton-Attwell, Kock & van Eeden (1970), Te (1974), and Turner & Clench (1974).

The list below shows the revised nomenclature of Michigan Physidae based on my own studies of shell and anatomy.

1. *Aplexa hypnorum* s.s. (Linné) 1758, *Syst. Natur.*, 10th ed., p 727 (= *elongata* Say 1821 + *glabra* Dekay 1843 + *elongatina* Lewis 1855 + *arctica* Clessin 1886 + *pilsbryi* Brooks 1935; European synonyms are excluded)
   Type locality: Europe, not specific.
2. *Aplexa hypnorum tryoni* (Currier) 1867, *Amer. J. Conchol.*, 3: 112
   Type locality: Grand Rapids, Kent Co., Michigan.
3. *Physa jennessi skinneri* (Taylor) 1954, *Occ. Paps. Mus. Zool., Univ. Mich.*, (557): 9 (= *elliptica minor* Crandall 1901 + *aplectoides* Sterki 1907 (*nomen nudum*))
   Type locality: Berends fauna (Pleistocene), SE cor. Sec. 6, T. 5 N., R. 28 E., Beaver Co., Oklahoma.
4. *Physa gyrina* s.s. Say 1821, *J. Acad. natur. Sci. Philad.*, 2: 171 (= *altonensis* Lea 1864 + *byersi* Crabb 1927 (*nomen nudum*))
   Type locality: Bowyer Creek, near Council Bluff[s], Iowa.
5. *Physa gyrina elliptica* (Lea) 1837, *Trans. Amer. phil. Soc.*, 5: 115 (= *smithsoniana* Lea 1864 + *febigeri* Lea 1864 + *elliptica deformis* Currier 1867)
   Type locality: Cincinnati, Ohio.
6. *Physa gyrina hildrethiana* (Lea) 1841, *Proc. Amer. phil. Soc.*, 2: 32
   Type locality: Illinois.
7. *Physa sayii* s.s. Tappan 1838, *Amer. J. Sci.*, 35: 269
   Type locality: Lake Pipin (as in original litt., not Pepin), Portage Co., Ohio.
8. *Physa sayii vinosa* (Gould) 1847, *Proc. Bost. Soc. natur. Hist.*, 2: 263
   Type locality: Lake Superior.
9. *Physa sayii magnalacustris* (Walker) 1901, *Nautilus*, 14: 97 (= *crassa* Walker 1901)
   Type locality: Frankfort, Benzie Co., Michigan.

TABLE 2. Species names of Physidae listed in molluscan surveys and catalogs of Michigan.

Physa	Annotations[1]
Physa anatina	Misidentification[2]
Physa ancillaria	Misidentification[3]
Physa aplectoides	= *Physa jennessi skinneri*
Physa brevispira	= *Physa integra brevispira*
Physa crandalli	Misidentification[4]
Physa deformis	= *Physa gyrina elliptica*
Physa elliptica	= *Physa gyrina elliptica*
Physa elliptica minor	= *Physa jennessi skinneri*
Physa febigeri	= *Physa gyrina elliptica*
Physa gyrina	-
Physa gyrina hildrethiana	-
Physa heterostropha	Misidentification[5]
Physa integra	-
Physa integra billingsi	= *Physa integra brevispira*
Physa lordi	Misidentification[6]
Physa magnalacustris	= *Physa sayii magnalacustris*
Physa michiganensis	= *Physa integra walkeri*
Physa microstoma	Misidentification[7]
Physa niagarensis	= *Physa integra brevispira*
Physa oleacea	Misidentification[8]
Physa oneida	Misidentification[9]
Physa parkeri	-
Physa pomilia showalteri	Misidentification[10]
Physa rhomboidea	Misidentification[11]
Physa sayii	-
Physa sayii crassa	= *Physa sayii magnalacustris*
Physa vinosa	= *Physa sayii vinosa*
Physa walkeri	= *Physa integra walkeri*
Physa warreniana	Misidentification[12]
Aplexa	
Aplexa distorta	Misidentification[13]
Aplexa elongata	= *Aplexa hypnorum*
Aplexa hypnorum	-
Aplexa hypnorum glabra	= *Aplexa hypnorum*
Aplexa hypnorum tryoni	-

[1] Annotations are based on a family-wide taxonomic study. Many of the names registered in these surveys and catalogs belong to taxa whose range does not extend to Michigan. They therefore represent misidentifications of one of the 14 Michigan entities. Many of these misidentifications have been pointed out by earlier workers. Except for *Physa crandalli*, *P. deformis*, *P. heterostropha*, *Aplexa hypnorum* and *A. hypnorum glabra*, type specimens of all the names listed above have been studied by the author.

[2] *P. anatina*; subspecies of *P. virgata*; distribution: Southwestern North America; probably misidentified *P. integra walkeri* in Michigan surveys.

TABLE 2. (Cont.)

[3]*P. ancillaria*; distribution: East coast of N. America; probably misidentified *Physa sayii vinosa*.

[4]*P. crandalli*; synonym of *P. aurea albofilata*; distribution: Southeastern U.S.; probably misidentified *P. sayii*.

[5]*P. heterostropha*; distribution: East coast of N. America; historically confused with *P. gyrina*; probably misidentified *P. integra walkeri*.

[6]*P. lordi*; distribution: Northwestern N. America; probably misidentified *P. parkeri*.

[7]*P. microstoma*; distribution: Southeastern U.S.; this species may be in subspecific relation with *P. aurea*; probably misidentified *P. gyrina elliptica*.

[8]*P. oleacea*; synonym of *P. aurea*; distribution: Southeastern U.S.; probably misidentified *P. gyrina elliptica*.

[9]*P. oneida*; synonym of *P. sayii alba*; distribution: Northeastern N. America; probably misidentified *P. sayii*.

[10]*P. pomilia showaltèri*; synonym of *P. pomilia*; distribution: Southeastern U.S.; probably misidentified *P. integra*.

[11]*P. rhomboidea*; synonym of *P. aurea albofilata*; distribution: Southeastern U.S.; probably misidentified *P. sayii*.

[12]*P. warreniana*; synonym of *P. ampullacea*; distribution: Northwestern N. America; probably misidentified *P. sayii*.

[13]*A. distorta*; listed as *Aplexa* in surveys, is *Physa distorta* in type specimen and species description; not a Physidae, but a synonym of *Bulinus contortus*; distribution: Southern Europe; probably misidentified *P. integra* in early Michigan surveys. I have examined Haldeman's type of *Physa distorta* and agree with Clench's (1930) remarks.

10. *Physa parkeri* s.s. "Currier" DeCamp 1881, *Kent Sci. Inst. misc. Publ.*,(5): 15 (Currier, 1868, *Kent Sci. Inst. misc. Publ.*, (7), no description)
Type locality: Houghton Lake, Roscommon Co., Michigan.
11. *Physa parkeri latchfordi* (Baker) 1928, *Wisc. geol. and natur. Hist. Surv., Bull.* 70, pt. 1: 423 (= *laphami* Baker 1928)
Type locality: Meach Lake, Ottawa Co., Quebec.
12. *Physa integra* s.s. Haldeman 1841, *A monogr. of the freshwater univalve Mollusca of U.S.*, (3): 3 of cover; 1842, *Monogr.* No. 6: 33
Type locality: Indiana.
13. *Physa integra brevispira* (Lea) 1864, *Proc. Acad. natur. Sci. Philad.*,(1864): 116 (= *niagarensis* Lea 1864 + *billingsi* Heron 1880)
Type locality: Ottawa River, Ontario.
14. *Physa integra walkeri* (Crandall) 1901, *Nautilus*, 15: 57 (= *michiganensis* Clench 1926 + *obrussoides* Baker 1928)
Type locality: Petosky, Emmet Co., Michigan.

THE PENIAL COMPLEX

A total of 252 alcohol lots are involved in this study. Table 5 shows the summary

TABLE 3. Biological studies relevant to Michigan Physidae.

Taxa	Authors	Year of publication	Subjects
Physidae (general)	Dawson	1911	Ecology and life history
	Wall	1968	Parasitology
Aplexa hypnorum	Hartog & Wolf	1962	Life history
	Vlasblom	1971	Ecology and life history
Physa gyrina	Thompson	1917	Behavior
	Crabb, E. D.	1927	Genetics
	Agersborg	1932	Ecology
	Dewitt	1954a, b, c	Life history
	Dewitt	1955	Ecology and life history
	Burch & Bush	1960	Cytogenetics
	Clampitt	1970	Ecology and life history
	van der Schalie & Berry	1973	Ecology
Physa sayii	Crabb, E. D.	1927	Genetics
	Crabb, E. D. & Crabb, R. M.	1927	Embryology
Physa parkeri	Cort *et al.*	1941	Parasitology
	Clampitt	1973	Ecology and life history
Physa integra	Ingram *et al.*	1958	Ecology
	Bickel	1965	Ecology
	Clampitt	1970, 1973	Ecology and life history

of results of the study on the gross morphology of the penial complex. Only a single specimen in each lot was dissected. Each penial complex was dissected out of the animal body, drawn with the aid of camera lucida and compared. Specimens are from museum alcohol collections, as well as from direct field collections. All specimens were identified as being true to type specimens by the author. Most of the specimens have been relaxed with menthol or nembutol, fixed in 10% formalin and preserved in 70% ethanol. Fig. 2 illustrates some of the important features of the penial complex that are useful for identification.

The terms "glandular" and "non-glandular", as they apply to the nature of the penial sheath, refer to observations of the whole penial complex as seen from the outside while using a Wild dissecting microscope (up to 50X). Histological sections of *Physa gyrina* show that even in the "non-glandular" half (NG) of the penial sheath, glandular cells are present; however, they are sparse and definitely not as developed and swollen as those found in the "glandular" half (G). Seen from the outside, without histological treatment, the terms "non-glandular" and "glandular" describe accurately the appearance of the penial sheath. The present designations of glandular (g), non-glandular (ng) and part glandular (pg) types of penial sheaths denote diagnostic differences in adult animals which are consistent for the family Physidae. This has been substantiated by the results of anatomical studies on 833 lots of reproductively mature specimens representing diverse conchological and geographic origins.

The types of penial sheaths further correlate with the types of spires on the shells (Te, 1974): they also correlate with observations on differences in the renal

FIG. 1. Distribution of *Physa sayii magnalacustris* in Michigan.

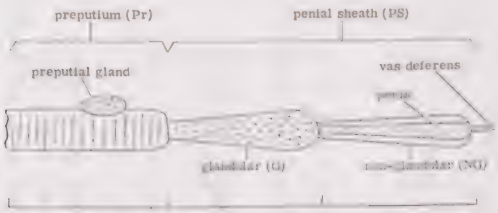


FIG. 2. Penial complex of *Physa sayii* s.s., an example of a "part-glandular" (pg) type of penial sheath.

complex, mantle digitations, mantle border, radula and other anatomical structures (Te, unpubl.).

SPECIES RELATIONSHIPS AND SYSTEMATIC NOTES

Group I

Aplexa hypnorum s.s. is quite distinct from the rest of the Michigan species of *Physa;* its closest relatives are *Stenophysa* of Central and South America. A wide gap now separates the distributional range of *Aplexa* from *Stenophysa*. *A. hypnorum tryoni* is a giant form of *A. hypnorum* s.s., but more studies are needed before the name is totally relegated to synonymy.

Group II

Physa jennessi skinneri[1] is related to *P. fontinalis* of the Palaearctic. The distribution range of *P. j. skinneri* is currently restricted to boreal North America and rarely extends below the 40th parallel of north latitude.

Group III

Physa gyrina, P. sayii and *P. parkeri* are all related in one species complex (Te, unpubl.). As such, there are intermediate forms that may be difficult to place; this is especially a problem between *P. gyrina* and *P. sayii*. Other major constituents

[1] More recent anatomical observations indicate that *skinneri* may be specifically distinct from *P. jennessi* s.s. However, more study is needed before this point is definitely settled.

TABLE 4. Species and subspecies of Michigan Physidae.[1,2]

	Lots from Michigan	Lots from other states	Habitat preference	Michigan distribution	General distribution
Aplexa					
Aplexa hypnorum s.s.	171	199	Woods pool	General	Circumboreal (above 40° N lat.)
Aplexa h. tryoni[3]	17	30	Woods pool	General	Boreal N. America (above 40° N lat.)
Physa					
Type a penial sheath: (see Table 5)					
Physa jennessi skinneri	6	42	Lakes	see footnote 4	Boreal N. America (spotty distribution; above 40° N lat.)
Type b penial sheath: (see Table 5)					
Physa gyrina s.s.	343	220	Ponds and ditches	General	Great Lakes region
Physa g. elliptica[3]	126	114	Creeks and brooks	General	Great Lakes region
Physa g. hildrethiana[3]	47	59	Woods pool, ponds and ditches	General	Great Lakes region
Physa sayii s.s.	635	389	Lakes and rivers	General	Great Lakes region
Physa s. vinosa[3]	163	173	Shore of the Great Lakes and large lakes	General	Great Lakes region
Physa s. magnalacustris[3]	104	24	Large lakes	see footnote 5	Great Lakes region

TABLE 4. (Cont.)

	Lots from Michigan	Lots from other states	Habitat preference	Michigan distribution	General distribution
Physa parkeri s.s.	22	1	Large lakes	see footnote 6	Endemic. Michigan
Physa p. latchfordi[3]	7	41	Large lakes	see footnote 7	Great Lakes region
Type c penial sheath: (see Table 5)					
Physa integra s.s.	389	234	Rivers	General	Great Lakes region
Physa i. brevispira[3]	65	79	Rivers and lakes	General	Great Lakes region
Physa i. walkeri[3]	130	58	Creeks and streams	General	Great Lakes region
TOTAL	2225	+ 1663	= 3888 lots examined		

[1]As ascertained from the collections of the Museum of Zoology, The University of Michigan.

[2]Type specimens of all taxa listed have been studied (except for *Aplexa hypnorum* s.s.).

[3]= Ecological subspecies (see Mayr, 1970).

[4]*Physa jennessi skinneri*: reidentified UMMZ specimens show the following distribution records for Michigan: Saginaw Bay, Wenona Beach, Bay Co.; Tamarack swamp, Isle Royale; Portage Lake, Jackson Co.; Grand Rapids, Kent Co.; Silver Lake and West Bloomfield, Oakland Co.; Manistique, Schoolcraft Co.; Four-mile Lake and South Lake, Washtenaw Co.

[5]*Physa sayii magnalacustris*: mostly found in large lakes along coastal counties of Michigan (see Fig. 1). Exceptions are: Higgins Lake and Houghton Lake, Roscommon Co.; Crystal Lake, Montcalm Co.; Margrethe Lake, Crawford Co.

[6]*Physa parkeri* s.s.: Douglas Lake, Cheboygan Co.; Long Lake, Grand Traverse Co.; Lake Huron, Sand Point, Huron Co.; Little Lake, Marquette Co.; Houghton Lake and Higgins Lake, Roscommon Co.

[7]*Physa parkeri latchfordi*: Saginaw Bay, Bay Co.; Gogebic Lake and Ontonagon River, Gogebic Co.; Saginaw Bay, Sand Point, Huron Co.; Gogebic Lake, Ontonagon Co.

TABLE 5. Penial complex of Michigan Physidae.

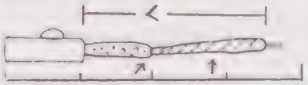
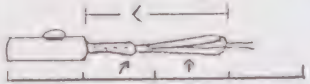
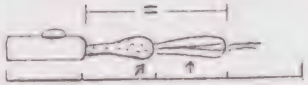
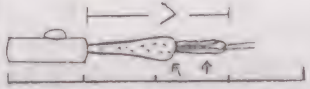
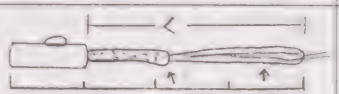
Taxa	Penial complex[1]	A[2]	B	C	D	E	F	Other information[3]
I. *Aplexa*-type:								
Aplexa hypnorum s.s.		22	4	-	3	g	3	Short terminal part of the penial sheath tends to be less glandular
A. h. tryoni		5	0					
II. *Physa* - Type a penial sheath:								
Physa jennessi skinneri		2	7	+	1	g	3	Penial sheath heavily swollen terminally
III. *Physa* - Type b penial sheath:								
A. 1. *Physa gyrina* s.s.		20	5	+	2	pg	2 1/2	NG > G[3]
P. g. hildrethiana		20	1					NG not transparent G not terminally swollen
2. *P. gyrina elliptica*		8	3	+	2	pg	2	NG > G NG transparent G not terminally swollen
B. 1. *P. sayii* s.s.		49	3	+	2	pg	2	NG = G NG transparent G terminally swollen
2. *P. sayii magnalacustris*		9	2	+	2	pg	2	NG < G NG transparent
P. s. vinosa		23	4					NG slender and short G terminally swollen

TABLE 5. (Cont.)

Taxa	Penial complex[1]	A[2]	B	C	D	E	F	Other information[3]
C. *P. parkeri*		12	0	+	2	pg	3	NG > G
P. p. latchfordi		0	1					NG transparent G not terminally swollen
IV. *Physa* - Type c penial sheath:								
1. *P. integra* s.s.		29	7	+	1	ng	1 1/2	PS swollen terminally
P. i. walkeri		5	0					
?. *P. integra brevispira*		8	3	+	1	ng	1 1/2	PS heavily swollen terminally
TOTAL		212 + 40 = 252 lots						

[1]In each of the figures in this column, the scale lines do not represent absolute measurements but relative lengths in relation to the preputium (pr), which is taken as the length of one scale.

[2]A = number of lots dissected of Michigan specimens; B = number of lots dissected from other states; C = preputial gland: present (+), absent (-); D = penial sheath partition: single part (1), 2-parted (2), 3-parted (3); E = glandular nature of penial sheath: fully glandular (g), part glandular (pg), not glandular (ng); F = ratio of penial sheath length to length of preputium, PS/Pr.

[3]See Fig. 2 for G, NG, PS.

TABLE 6. Conchological characters and character states of Michigan Physidae.[1]

Characters	Taxa													
	hypno	tryon	skinn	gyrin	ellip	hildr	sayii	vinos	magna	parke	latch	integ	brevi	walke
I. Whole shell characters:														
A. Shell shape & whorl number:														
Shell shape	ES	ES	EC	EC	EC	EC	OG	OG	GS	GS	GS	EO	EO	EO
Whorl number	5-7	5-7	4	5	5	5	5	4	5	5	5	4-5	4-5	5
B. Shell dimensions:														
Shell length (mm)	12.5	23	9.3	15	12.7	23.7	19.2	16.3	15.7	24	18.2	12.7	10.8	10.5
SW/SL	.39	.38	.48	.52	.55	.51	.65	.67	.71	.76	.81	.63	.68	.59
AW/AL	.52	.51	.50	.52	.51	.58	.55	.64	.53	.61	.64	.57	.60	.53
SpL/SL	.47	.51	.32	.31	.28	.37	.19	.26	.16	.15	.14	.26	.23	.32
aSpL/SL	.28	.29	.20	.17	.12	.22	.12	.10	.08	.10	.07	.12	.11	.17
C. Qualitative characters:														
Translucency	Tr	Tr	Tr	Op	Op	Op	Op	Op	n	Op	Op	Op	n	Op
Glossiness	Gl	Gl	Gl	Sh	Sh	Sh	Sh	Sh	dul	Sh	Sh	Sh	Sh	Sh
Shell color	Hr	Hr	Hr	Hr	Hr	Hr	Hr	RHr	Wh	Wh	YHr	Hr	Wh	Hr
Spiral striation	n	n	n	H	H	H	Sb	Sb	sl	sl	Sb	n	n	sl
Shell thickness	t	t	t	Rg	Rg	Rg	Rg	s	S	s	Rg	s	S	Rg
Columella fold	Rg	Rg	Rg	Rg	Th	Rg	Rg	Th	Th	Th	Th	Th	Th	Rg
Parietal callus	Nr	Nr	vWd	Rg	Rg	Rg	Wd	Wd	Wd	Wd	Wd	Rg	Rg	Nr
Shouldering	n	n	n	sl	sl	sl	sl	sl	H	An	H	sl	H	sl
Rest callus	n	n	n	H	H	H	Pr	Pr	Pr	n	n	H	H	H
II. Aperture characters:														
Aperture shape	lS	lS	lS	lS	lS	lS	nrOL	nrOL	nrOL	brOL	brOL	eS	eS	eS
Aperture size	Nr	Nr	Nr	Rg	Nr	Rg	Wd	Wd	Wd	Wd	Wd	Wd	Wd	Rg
Displacement	n	n	n	n	n	n	n	Ds	Ds	Ds	Ds	n	Ds	n

TABLE 6. (Cont.)

Characters	Taxa													
	hypno	tryon	skinn	gyrin	ellip	hildr	sayii	vinos	magna	parke	latch	integ	brevi	walke
Outer lip	t	t	t	Rg	Rg	Rg	t	Rg	Th	Th	Th	Th	Th	Rg
Callus color	Wh	Wh	n	R/Wh	R/Wh	R/Wh	n	R/Wh	R/Wh	R/Wh	R/Wh	Wh	Wh	n
Insertion angle	Sm	Sm	Sm	Sm	Sm	Sm	Sm	Sm	Sm	Sm	Sm	An	An	An
III. Spire characters:														
Spire shape	E	E	Bl	C	C	C	Dp	Dp	Dp	Dp	Dp	I	I	I
Spire angle	45°	45°	60°	75°	75°	65°	85°	100°	120°	130°	115°	80°	90°	60°
Indentation	so	so	so	Rg	Rg	Rg	sl	sl	sl	sl	sl	St	St	St
Sutural slope	Inc	Inc	sl	sl	sl	sl	sl	sl	n	n	n	sl	n	sl
Subsutural band	Br	Br	Wh	Y-Wh	Wh	Y-Wh	Wh	Y-Wh	Wh	Wh	Wh	Wh	Wh	Wh
Protoconch shape	Rd	Rd	Bl	Sp	Sp	Sp	Sp	Sp	Sp	Sp	Sp	Sp	Sp	Sp
Protoconch color	Dr	Dr	Rg	Rg	Rg	Rg	dS	dS	Dr	Dr	Dr	dS	Dr	dS

[1] Part of the author's basic data matrix for the family Physidae intended for computer evaluation of taxonomic distance. They are provided here to supplement the keys. The data are not averages, but represent measurements of a single typical (not type) Michigan lot per taxon.

brevi = *P. integra brevispira*; ellip = *P. gyrina elliptica*; gyrin = *P. gyrina* s.s.; hildr = *P. gyrina hildrethiana*; hypno = *A. hypnorum* s.s.; integ = *P. integra* s.s.; latch = *P. parkeri latchfordi*; magna = *P. sayii magnalacustris*; parke = *P. parkeri* s.s.; sayii = *P. sayii* s.s.; skinn = *P. jennessi skinneri*; tryon = *A. hypnorum tryoni*; vinos = *P. sayii vinosa*; walke = *P. integra walkeri*.

An = angled, angulate; Bl = blunt; Br = brown; brOL = broadly ovate-lunate; C = acute-conical; Dp = depressed; Dr = definitely dark, purplish; ds = darker than shell; Ds = displaced; dul = dull; E = acute-elongate; EC = elliptical-subcylindrical; EO = elongate-ovate; eS = ear-shaped; ES = elongate-slender; Gl = glossy-polished; GS = globose-shouldered; H = heavy; Hr = horn; I = acute-indented; Inc = inclined; lS = loop-shaped; n = none; nrOL = narrowly ovate-lunate; Nr = narrow; OG = ovate-globose; Op = translucent; Pr = present but not obvious; Rd = rounded-exerted; Rg = regular; RHr = reddish-horn; R/Wh = reddish to white; s = somewhat solid; S = solid, thick; Sb = subobsolete; Sh = shiny; Sl = slight; Sm = smooth; so = some; Sp = pointed-conical; St = strong; t = thin; Th = thick; Tr = transparent; vWd = very wide; Wd = wide; Wh = white; YHr = yellowish-horn; Y-Wh = yellowish to white.

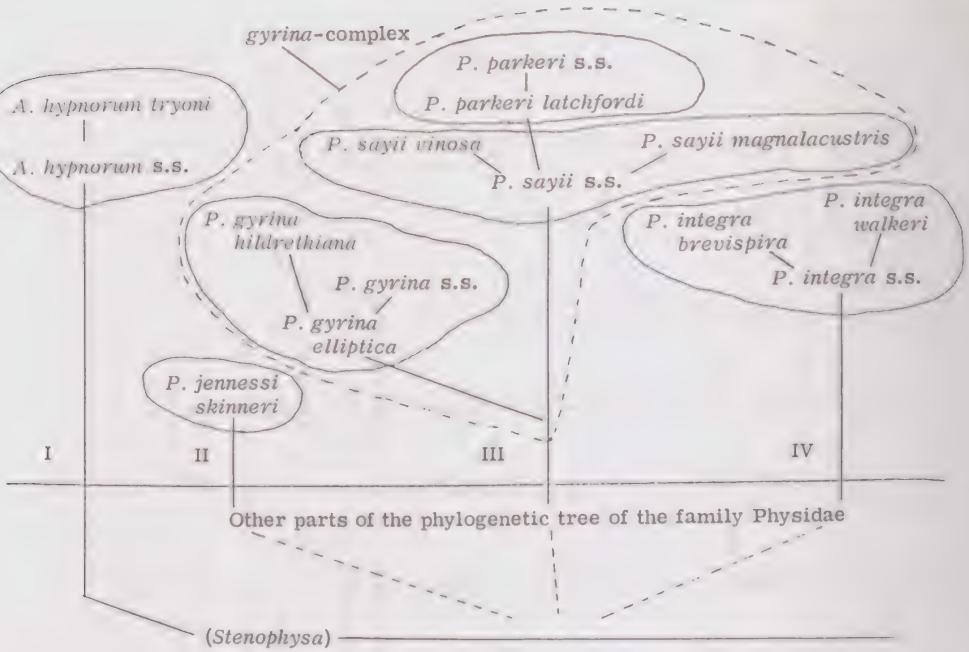


FIG. 3. A partial phylogenetic tree for Michigan Physidae.

of this complex (not found in Michigan) are *P. ampullacea* and *P. aurea*.

Group III and Group IV correspond to F. C. Baker's (1926, 1928) 2 anatomical groupings and are very distinct anatomically from Groups I and II. Both Group III and Group IV have undergone extensive diversification in North America.

Group IV

Physa integra is the only species of this group found in Michigan. Group IV species are mostly found in more southern latitudes; *P. pomilia*, *P. osculans*, *P. virgata*, *P. humerosa*, *P. squalida* are some examples. *Physa acuta* of southern Europe and the Mediterranean regions belongs to Group IV.

Systematic notes on *Physella* and *Physodon*

The generic or subgeneric designation of *Physella* and *Physodon* to Group III and IV respectively (sensu F. C. Baker, 1928) is currently being critically evaluated. F. C. Baker (1926, 1928, in Baker & Cahn, 1931) left the question unresolved. My anatomical studies show that *Physa microstoma*, the type species of *Physodon*, is anatomically a member of Group III. Baker (1926, 1928) consigned *P. microstoma* to what I call Group IV, without checking the anatomy and through erroneous conchological association (Te, unpubl. data). The *P. microstoma* that I studied are from Tennessee, the center of the distribution range of this species. Conchologically, it agrees perfectly with Haldeman's type specimen (lodged at ANSP), including having the 2 tooth-like calluses on the columella (diagnostic character), which indicate certainty of equivalence to Haldeman's species.

F. C. Baker emended the names *Physella* and *Physodon* from Haldeman (1842) for his 2 anatomical groups. Clench (1930: 306) considered this problem and was strongly critical of F. C. Baker's emendation of subgeneric names: "Emendation of previous names, especially when such are not based on the original materials are prone to lead to serious errors." Baker's reply (in Baker & Cahn, 1931) on

this point is unsatisfactory and confusing. The *Physella gyrina* in his 1928 (p 417, 449) Wisconsin monograph (technically *Physella* (*Physella*) *gyrina*) was precipitously changed in this 1931 paper to *Physa* (*Physodon*) *gyrina*. In theory, after Baker's 1926 emendations, both "*Physella*" and "*Physodon*" have acquired anatomical connotations at the subgeneric level. When the same *gyrina* is switched from "*Physella*" to "*Physodon*", for nomenclatural reasons and to circumvent criticism, one is left confused as to where the anatomy stands. At present, the soft parts of *P. globosa* (type species of *Physella*) are not available to me for study; for the time being, therefore, and until a detailed anatomical study of *P. globosa* can be made, the use of *Physella* and *Physodon* in place of *Physa* should be avoided.

Despite Clench's criticisms, Baker's observation of 2 types of male genitalia for dividing American *Physa* into 2 natural groups is accurate (Clampitt, 1970; Te, 1974). The problem comes with the emendation of names and not with the anatomical facts. Baker's observations on the differences between the European *P. fontinalis* and "American species" in terms of mantle digitation and radular dentition are likewise accurate (Te, unpubl. observations). It is worth mentioning that Baker did not examine the male genitalia of *P. fontinalis*, for had he done so, he would have added this 3rd character, which can be correlated with the differences in mantle types and radular dentition (Te, unpubl.).

Additionally, Baker did not observe *Physa jennessi skinneri*, a species known then as *P. aplectoides* (*nomen nudum*) from Ohio and northern Michigan. Had Baker done so, he would have recognized that "*P. aplectoides*" falls naturally into a group with *P. fontinalis* (Te, 1974) and is unlike the rest of the "American *Physa*".

In summary, it can be stated that the majority of North American *Physa* species do indeed form 2 natural anatomical groups, as Baker had observed. *P. jennessi* and its geographic subspecies, however, are allied to *P. fontinalis* of the Palaearctic and with it form a 3rd group. The taxonomic significance of these 3 groups must be evaluated very carefully to avoid repeating mistakes of past malacologists. Clench's 1930 cogent criticism (as quoted above), which proved accurate and farsighted, in view of the facts known to me now, should be a fair warning against haste.

A CONCHOLOGICAL KEY TO MICHIGAN PHYSIDAE

In place of shell ratios, the general shell shape is emphasized in the key below. It is therefore absolutely necessary to check the text figures when figures are referred to. In all cases, judgements should be made after allowing for variability; also, anatomical and ecological information should be considered when such data are available. In difficult cases, the user should refer to the partial phylogenetic tree in Fig. 3 to narrow down alternatives; then the specimens should be compared with characters listed in Table 6; and the final decision should be based on multiple character concordance.

For general purposes, keying down to the species, and the geographic subspecies in the case of *Physa jennessi skinneri*, is sufficient, although the key includes ecological subspecies. The validity of "ecological subspecies" taxa is still a debated problem in systematics. Subspecific differences (geographical and ecological) are by nature statistical in diagnosis. This situation has been stated in many recent standard books on evolutionary and systematic biology. To key down to the ecological units, all of the specimens of a lot should be considered; a majority agreement (both in characters and specimens) points to a particular trinomen. When characters and specimens of a lot are equivocal between 2 subspecific taxa, the situation should be cited, the species name (*sensu lato*) retained and the trinomen not used.

(The author expresses his thanks to the several persons who spent their time testing the key. Their many suggestions have resulted in considerable improvement.)

		Species and geographical subspecies	Ecological subspecies
1a.	Shell slender (elongate or elliptical in shape as in Figs. 4a,b,c); shell with an "oily" gloss; protoconch rounded, exerted or flat-obtuse (blunt) (Fig. 11). (If shell as in Fig. 4c, it is thin and transparent and the protoconch is flat-obtuse (blunt)) 2		
1b.	Shell not slender (shell elliptical, globose or ovate in shape as in Figs. 4d-4n); shell not "oily"; protoconch pointed conical (Fig. 11) 3		
2a.	Shell elongate-slender (Figs. 4a,b); shell whorls 5 or more; spire long, almost half the shell length; protoconch dark in color, rounded knob-like; subsutural line brown; parietal callus narrow	*A. hypnorum*	A
2b.	Shell elliptical-subcylindrical (Fig. 4c); shell whorls 4 or less; spire about 2/5 of shell length or less; protoconch same color as body whorl, flat-obtuse (blunt); subsutural line white; parietal callus very wide	*P. jennessi skinneri*	
3a.	Shell elliptical or globose (Figs. 4d-4k); suture not strongly indented (Fig. 5) 4		
3b.	Shell elongate-ovate (Figs. 4l,m,n); sutures strongly indented (Fig. 5)	*P. integra*	B
4a.	Shell globose (Figs. 4g-4k); parietal callus wide (Fig. 10); spire depressed; aperture ovate-lunate, expanded (Fig. 6) 5		
4b.	Shell elliptical-subcylindrical (Figs. 4d,e,f); parietal callus not wide (Fig. 10); spire not depressed (if depressed, shell width is less than 8 mm, shell more elliptical than globose); aperture loop-shaped and not expanded (Fig. 6).	*P. gyrina*	C
5a.	Shell globose, heavily shouldered and exceeding 18 mm in length (Figs. 4j,k); aperture shape broadly ovate-lunate (Fig. 6); protoconch dark purplish (must be large shell, over 18 mm).	*P. parkeri*.	D
5b.	Shell globose, and if heavily shouldered, is less than 18 mm in length (Figs. 4g,h,i); aperture shape narrowly ovate-lunate (Fig. 6); protoconch darker than body whorl but not purplish (if purplish, shell length must be less than 18 mm).	*P. sayii*	E

A. Key to ecological subspecies of *Aplexa hypnorum:*

1a. Shell length over 20 mm (Fig. 4b). . . . . *A. hypnorum tryoni*
1b. Shell length less than 18 mm (Fig. 4a) . . . . . *A. hypnorum* s.s.

Ecological subspecies

B. Key to ecological subspecies of *Physa integra:*

1a. Shell solid, heavy, whitish; spire more depressed; protoconch distinctly dark or purplish (Fig. 4m) . . . . . *P. integra brevispira*

1b. Shell less solid, not heavy, horn colored; protoconch darker than shell, but not distinctly dark or purplish 2

2a. Shell more elongate, less ovate (Fig. 4n); spire longer. . . . . *P. integra walkeri*

2b. Shell more ovate (Fig. 4l); spire shorter. . . . . *P. integra* s.s.

C. Key to ecological subspecies of *Physa gyrina:*

1a. Shell more elliptical (Fig. 4e); spire more depressed; spiral striation subobsolete (Fig. 9) . . . . . *P. gyrina elliptica*

1b. Shell less elliptical (Figs. 4d,f); spire not depressed; spiral striation heavy (Fig. 9). 2

2a. Spire distinctly more elongate; penultimate whorl distinctly exerted (Fig. 4f) . . . . . *P. gyrina hildrethiana*

2b. Spire conical, less elongate; whorls on spire more regularly increasing, penultimate whorl thus appears less exerted (Fig. 4d). . . . . *P. gyrina* s.s.

D. Key to ecological subspecies of *Physa parkeri:*

1a. Shell whitish; more solid, heavier (Fig. 4j) . . . . . *P. parkeri* s.s.

1b. Shell horn to yellowish horn; less solid, light (Fig. 4k). . . . . *P. parkeri latchfordi*

E. Key to ecological subspecies of *Physa sayii:*

1a. Shell very thick, heavy, whitish; shouldering heavy; outer lip of aperture very thick; spire very depressed; spire convexly sloping toward the apex; protoconch dark purplish (Fig. 4i). . . . . *P. sayii magnalacustris*

1b. Shell not very thick, not heavy, horn colored; shoulder not heavy; outer lip of aperture not very thick; spire conical, not convexly sloping toward the apex; protoconch darker than shell, but not purplish (Figs. 4g,h) 2

2a. Columellar fold thick; body whorl widest toward the spire; shell more solid; aperture distinctly displaced to the left, shell not symmetrical (Fig. 4h) . . . . . *P. sayii vinosa*

2b. Columellar fold not thick; body whorl widest at about mid-section; shell not solid; aperture not displaced, shell symmetrical (Fig. 4g) . . . . . *P. sayii* s.s.

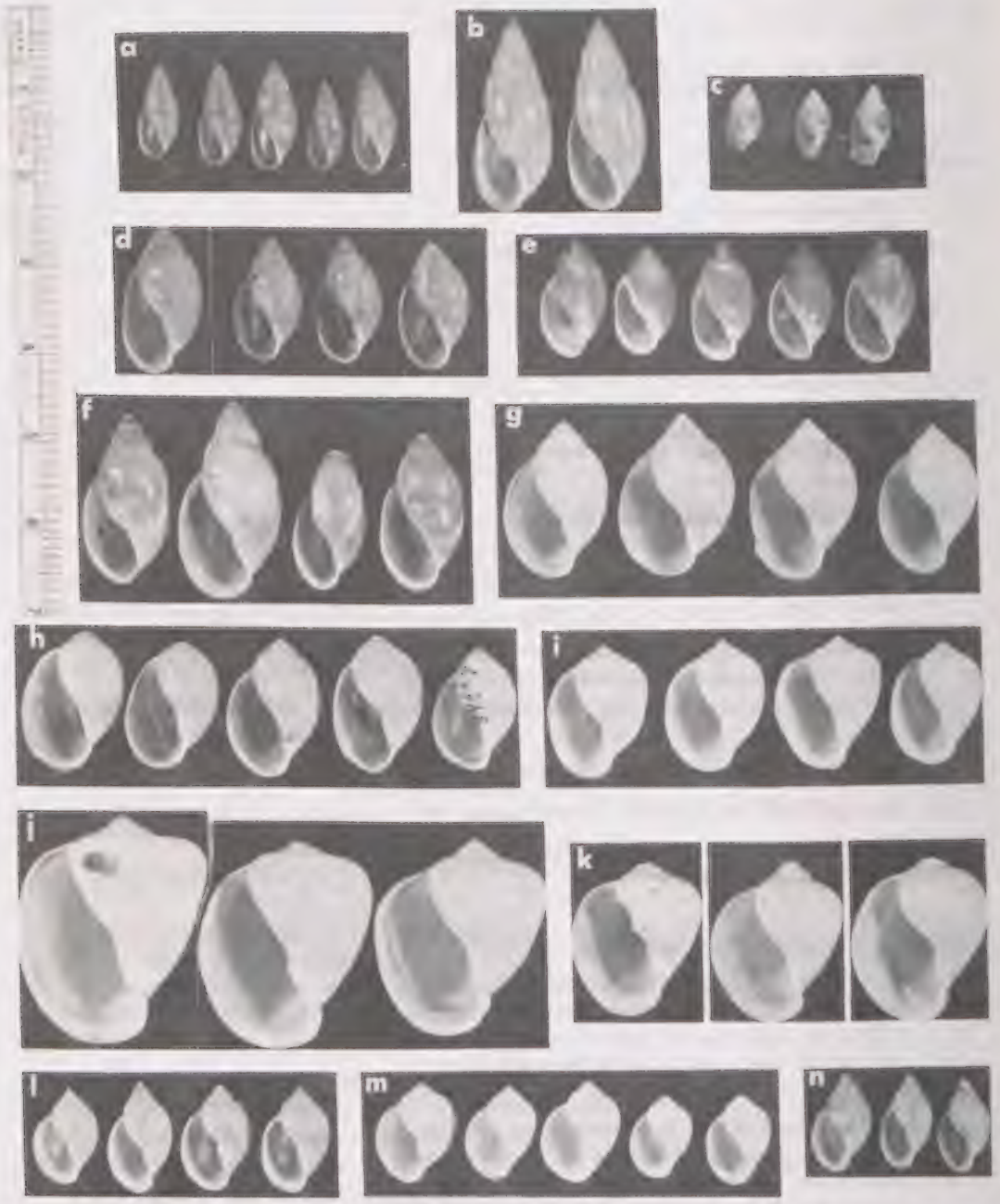
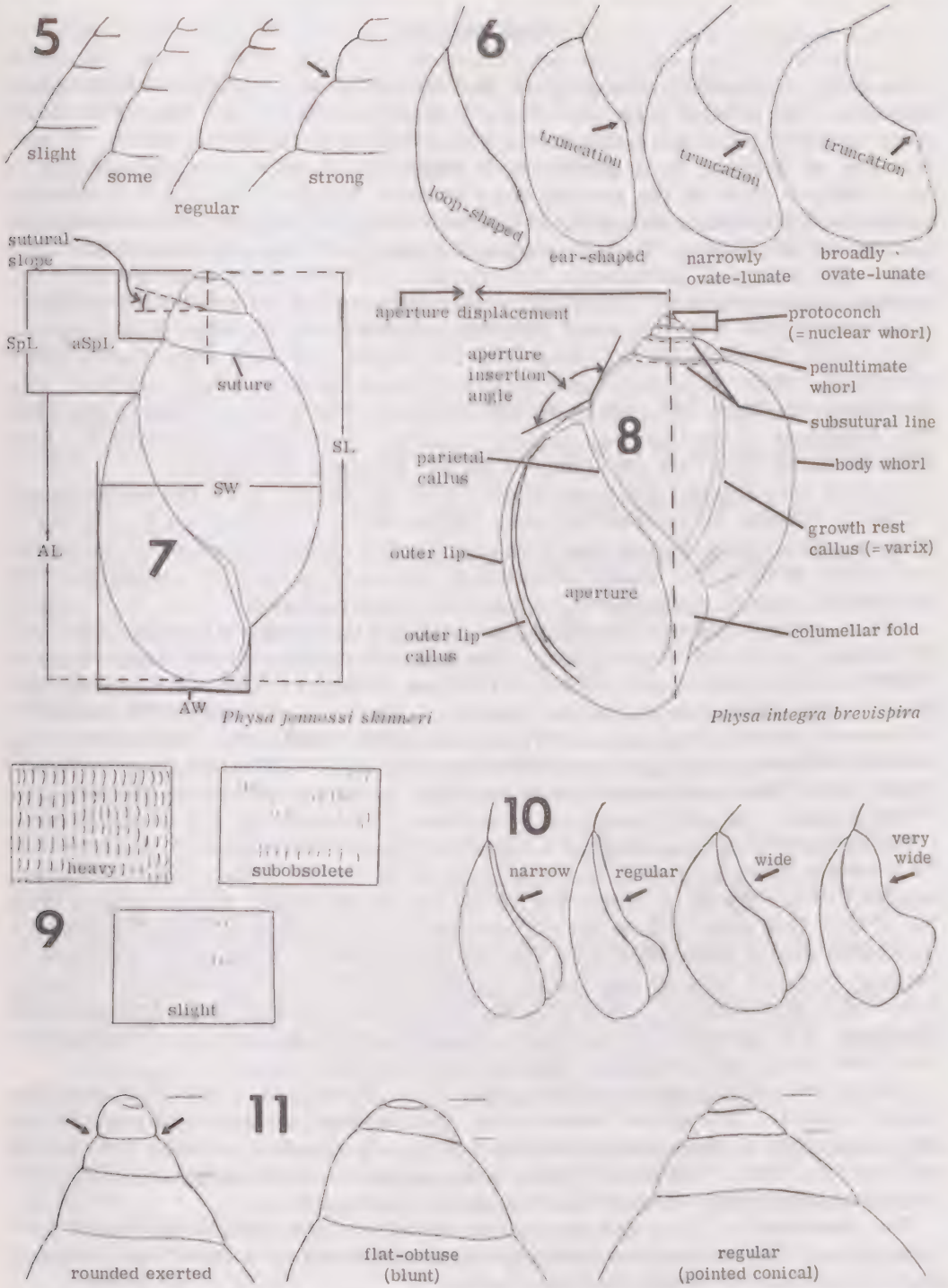


FIG. 4. Michigan Physidae. a, *Aplexa hypnorum* s.s. b, *A. hypnorum tryoni*. c, *Physa jennessi skinneri*. d, *P. gyrina* s.s. e, *P. gyrina elliptica*. f, *P. gyrina hildrethiana*. g, *P. sayii* s.s. h, *P. sayii vinosa*. i, *P. sayii magnalacustris*. j, *P. parkeri* s.s. k, *P. parkeri latchfordi*. l, *P. integra* s.s. m, *P. integra brevispira*. n, *P. integra walkeri*.



FIGS. 5–11. Shell terminology. FIG. 5. Suture indentation. FIG. 6. Aperture shape. FIG. 7. Shell dimension ratios. FIG. 8. Shell terminology. FIG. 9. Variation in spiral striation. FIG. 10. Parietal callus. FIG. 11. Protoconch shape. Abbreviations: AL = aperture length; aSpL = apical spire length; AW = aperture width; SL = spire length; SpL = spire length; SW = shell width.

DISCUSSION

Goodrich in his 1932 monograph of Michigan Mollusca recognized 5 species of Physidae. The present study adds *Physa jennessi skinneri* to his list. Four of the above belong to the Great Lakes fauna, while 2 belong to the boreal fauna. *P. parkeri* s.s. is endemic to Michigan and is restricted to only a few large lakes, but the *latchfordi* form of the species has a broader distribution. The 8 "ecological subspecies" included in this study are recognized in the interest of promoting further biological studies. These "ecological subspecies" show consistent and diagnostic morphological differences, but whether ecological subspecies deserve trinomenal names is still a debated question in systematics, as mentioned earlier.

Apparently, the most frequently encountered species of Physidae in Michigan is *Physa sayii*, followed by *P. gyrina* and *P. integra*. *Aplexa hypnorum* is 4th in occurrence, while *P. parkeri* and *P. jennessi skinneri* are the least common. This observation has been reported in the literature and it is also reflected in the relative abundance of museum specimens. Except for *P. parkeri latchfordi*, I have collected in the field live specimens of all the Michigan Physidae.

I concur with Clench (1925) that *Physa parkeri* is distinct from the northwestern *P. lordi*. Further, *P. sayii* should not be lumped with the East Coast *P. ancillaria*, as some authors have already done, following Wurtz's (1949) metric study on shells. Anatomical studies (Te, unpubl.) show that *P. sayii* differs from *P. ancillaria;* both are distinct from *P. heterostropha* sensu F. C. Baker (1928).

Physa jennessi skinneri from Michigan (shell and live material) agrees very well with Clarke's detailed description. The extant form also agrees very well with Walker's (1918) specimens (UMMZ 117539 and UMMZ 117538) of *"P. aplectoides* Sterki" from Isle Royale and School Craft Co., Michigan. (Sterki, 1907, named *P. aplectoides* following the opinion of Walker that it was "distinct".) The extant form, however, differs in size and shell ratios from the types of Pleistocene *P. skinneri* Taylor 1954. When a consensus is developed that the fossil *skinneri* is distinct, then *P. aplectoides*, presently inadequately described, stands ready for redescription.

The absence of a preputial gland in *Aplexa hypnorum* is important. *Stenophysa* of the southern hemisphere also lack this gland (H. B. Baker, 1930; Ranson & Cherbonnier, 1951; Harry & Hubendick, 1964; Richards, 1964; Starobogatov, 1967; Te, 1974). This clear anatomical disjunction, in comparison to *Physa*, suggests a taxonomic gap of substantial size. An overall numerical taxonomic evaluation of phenetic distance between the *Aplexa* groups and the *Physa* groups is currently underway. Starobogatov (1967) split the family into 2 subfamilies, Aplexinae and Physinae. It is important to see whether Starobogatov's decision can be supported when many characters and many taxa are considered at once.

The generic or subgeneric differentiation in *Physa* (*sensu lato*) has been discussed earlier. Anatomical bases exist, but the problem is one of emendation. The anatomy of *P. microstoma* is now known; *"Physodon"* belongs to Group III and not to Group IV as Baker would have placed it. A resolution of *"Physella"* awaits the availability of anatomical materials of *P. globosa*.

The conchological keys and anatomical references provided in this paper have been geared only to diagnose Michigan Physidae. The key is based on commonly encountered adult Michigan field specimens.

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BULINUS SERICINUS (GASTROPODA: PLANORBIDAE) FROM ETHIOPIA[1]

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ABSTRACT

Bulinus sericinus (Jickeli) was the 1st planorbid bulinine snail to be named from the Ethiopian highlands. Recently it was found to be a tetraploid (n=36, 2n=72) species, having twice the number of chromosomes of most members of the Planorbidae (x=18). In this way, it is cytologically similar to *B. truncatus* (Audouin) of the Near East and Africa north of the Sahara, which is also a tetraploid species as well as being the intermediate host of human schistosomiasis in much of its area of geographical distribution. The present study compares the morphology, esterase electrophoretic pattern and antigen-antibody reaction of *B. sericinus* to that of its better known neighbor to the north, *B. truncatus*. The population of *B. sericinus* studied was a laboratory-bred stock from the type locality of the species, the Toquor River at Mekerka, Ethiopia. The *B. truncatus* specimens used for comparison were also a laboratory-bred stock, originally from Iflaka Bilharzia Project area, Behaira Province, Egypt.

In general, the morphology of *Bulinus sericinus* is the same as that of *B. truncatus*. The differences between the 2 species are as follows: (1) The shells of *B. sericinus* were medium-spired (mean L/AL=1.39), had elongate-ovate apertures (mean AL/AW=1.9) and body whorl contours that were not markedly inflated; the shells of *B. truncatus* were high-spired (mean L/AL =1.52), had ovate apertures (mean AL/AW=1.68) and body whorl contours were markedly inflated; (2) The mantle pigmentation of *B. sericinus* was dark grey to black in irregular patches over a greyish background, and the tunica propria of the visceral hump was transparent, except for the area overlying the ovotestis; neither the mantle nor the tunica propria of *B. truncatus* was pigmented; (3) Five out of the 64 *B. sericinus* radulae showed an asymmetrical development of the rachidian cusps, while 38 out of 150 *B. truncatus* radulae showed the rachidian cusp deformity with either 1 or both cusps missing; (4) The numbers of lateral teeth of *B. sericinus* were always larger than those of *B. truncatus* of equivalent shell lengths; (5) Reproductive maturity (using the initial enlargement of the seminal vesicle as an indicator) of *B. sericinus* occurred at 6.8-7.0 mm shell length, while that of *B. truncatus* was attained at 4.6-5.0 mm shell length; (6) The percentage of euphallic specimens was low (1.8%) for *B. sericinus*, while it was high (15.2%) for *B. truncatus*.

Electrophoretically separated foot muscle esterases of both *B. sericinus* and *B. truncatus* were identical. The foot muscle antigen of *B. sericinus* tested against antisera for *B. truncatus* showed no 'non-identity' precipitin reactions.

Because of the close morphological similarities between the 2 populations, *Bulinus sericinus* is probably only a race of *B. truncatus*. Cross-breeding studies should shed further light on this suggestion.

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INTRODUCTION

Jickeli (1874) described 2 bulinine snails from the Ethiopian highlands: 1 specimen with a low spire was named *Isidora sericina*, while 4 specimens with high spires were named *I. schackoi*. Mandahl-Barth (1957) united these and several other forms described from Ethiopian localities under the name *Bulinus sericinus*, which he placed in the *B. tropicus* species group. *Bulinus sericinus* was later regarded as a subspecies of *B. truncatus* by Mandahl-Barth (1960, 1965) and by Brown (1965), although regarded as a distinct species, *B. sericinus*, by Wright & Brown (1962), and then completely synonomized under *B. truncatus* by Brown & Wright (1972).

The anatomy of *"Bulinus sericinus"* was reported from Senegal (Wright, 1956). However, Wright & Brown (1962), after reexamining their material, stated that the specimens should not have been referred to *B. sericinus*. They also studied the morphology of a population of *"B. sericinus"* from near Debra Markos, about 300 miles south of the type locality (Toquor River at Mekerka) of *B. sericinus*. However, in all of these previous reports (except for Brown & Wright, 1972) chromosome numbers of the taxa in question were left undetermined, a vital gap in the information necessary for species placement.

Burch (1967) speculated that topotype specimens of *Bulinus sericinus* might be tetraploid (n=36) and that *B. schackoi*, shown to be tetraploid, might be a synonym of *B. sericinus*. Later, he (Burch, 1969) reported topotypes of *B. sericinus* to be tetraploid (n=36, 2n=72). Thus, the 2 nominate forms, *B. schackoi* and *B. sericinus*, are both cytologically similar to *B. truncatus* (Audouin 1827) of the Near East and Africa north of the Sahara, which is also a tetraploid species (Burch, 1964) as well being the intermediate host of human schistosomiasis in much of its area of geographic distribution.

The cross breeding of *Bulinus sericinus* with a diploid albino strain of *B. tropicus* was studied by Wu (1972), and *B. sericinus* was experimentally infected with 4 strains of *Schistosoma haematobium* from Egypt, Iran, Liberia and Rhodesia by Wu & Burch (1974). However, neither morphological nor biochemical studies have been done on topotypical specimens of *B. sericinus*. The present work deals with the shells, pigmentation of animal, radula, reproductive system and the electrophoresis of foot muscle, and the results are compared to those of its better known neighbor to the north, *B. truncatus*, as described in a previous study (Wu, 1972).

MATERIALS AND METHODS

The population of *Bulinus sericinus* studied was a laboratory-bred stock from the type locality of the species, the Toquor River at Mekerka, Ethiopia. For comparison of electrophoretic patterns, the laboratory-bred *B. truncatus* from the Iflaka Bilharzia Project area, Behaira Province, Egypt, was used.

Shell. Shells were sorted into size groups termed the 3 mm group, the 4 mm group, etc. (e.g., the 3 mm group contained individuals of 3.1 - 4 mm shell length). Ninety-nine shells (2, 4, 10, 18, 30, 17, 12, 4 and 2 shells for the 3 mm to 11 mm size groups, respectively) were chosen and measured according to the method applied by Wu (1972). Means and standard deviations of the shell widths (W) and of the ratios of shell length/aperture length (L/AL), shell length/shell width (L/W) and aperture length/aperture width (AL/AW) for each size group and their grand means and standard deviations were calculated.

Pigmentation of animals. Snails were relaxed with menthol crystals in distilled water for 6-7 hours. The completely relaxed snails were later immersed in hot tap water (approximately 70-80°C) for 1 minute, then fixed and preserved in 30% ethanol. The shells were removed immediately either by twisting them off the animals, or by crushing them. Care was taken to minimize injury to the animal, especially when the shell had to be crushed.

Photographs were taken to show mantle markings and pigmentation of the tunica propria, the thin membrane overlying the visceral hump.

Radula. Sixty-four radulae were prepared according to the method of Wu (1972: 100). The teeth were drawn with the aid of a camera lucida. The shells of animals from which radulae were taken were sorted into mm size groups as described above. The shell length (L) and the number of lateral teeth in a half transverse row were recorded and a scatter diagram was prepared (Fig. 9).

Reproductive system. The entire reproductive system was dissected out, drawn and described for animals with shell lengths of 3, 4.6, 5.8, 6.8, 7.3 and 9 mm (1 animal from each shell size category). Estimations of surface ratios of albumen gland/prostate gland, spermatheca/prostate gland and ovotestis/albumen gland for each size group were made from the camera lucida drawings, the surface being that area shown in the drawing from the ventral side.

Electrophoresis. The foot muscle esterases of *Bulinus sericinus* and *B. truncatus* were compared. The electrophoretic technique applied was a modification of that described by Davis & Lindsay (1967). The diagrams (Fig. 17B) of foot muscle esterase bands were obtained from (1) direct visual inspection of the stained gels (Fig. 17A) and (2) densitometric tracings of the stained gels (Fig. 17C) made with a Photovolt Densicord Densitometer (Model 552).

Immunology. The technique was the same as that used by Burch & Lindsay (1970). Antigens from *Bulinus sericinus* were tested for 'identity' and 'non-identity' reactions with antisera for *B. truncatus* (Iflaka Bilharzia Project area, Behaira Province, Egypt) and *B. tropicus* (De Villiers cement reservoir, Malelane, Nelspruit, Transvaal, South Africa).

RESULTS

Shell morphology

The general shell morphology of *Bulinus sericinus* was the same as described for other bulinine shells (Wu, 1972). The spires were of medium height (with the mean of the ratios of shell length/aperture length (L/AL) being 1.39 and the range 1.28-1.53). The contours of the body whorl were not markedly inflated (see Fig. 1). The aperture shapes were elongate-ovate; the mean of the ratios of aperture length/aperture width (AL/AW) was 1.9 and the range was 1.85-2.17. The shells' color was light brown.

TABLE 1. Shell measurements of *Bulinus sericinus* and *B. truncatus*.

Size group (in mm)	*Bulinus sericinus*					*Bulinus truncatus*				
	n	L/AL	L/W	W	AL/AW	n	L/AL	L/W	W	AL/AW
3	2	1.39	1.66	1.98	1.85	2	1.36	1.35	2.60	1.63
4	4	1.28	1.57	3.13	2.13	4	1.43	1.47	3.33	1.85
5	10	1.34	1.54	3.58	2.05	10	1.52	1.42	3.92	1.67
6	18	1.34	1.51	4.35	1.95	18	1.50	1.43	4.60	1.69
7	30	1.40	1.54	4.87	1.97	30	1.53	1.45	5.24	1.68
8	17	1.44	1.65	5.16	2.00	17	1.55	1.43	5.99	1.62
9	12	1.49	1.65	5.75	1.86	8	1.55	1.48	6.38	1.69
10	4	1.50	1.69	6.22	1.99	3	1.68	1.52	6.83	1.68
11	2	1.53	1.89	6.11	2.17	2	1.54	1.46	7.90	1.66
	99					94				
Mean		1.39	1.57	4.71	1.90		1.53	1.44	5.18	1.68

n = number examined; L = shell length; W = shell width; AL = aperture length; AW = aperture width. The data on *Bulinus truncatus* are from Wu (1972).

FIG. 1. Shells of *Bulinus truncatus* (upper row) and *B. sericinus* (lower row) in aperture view. In both series the shells represent sizes from 3 to 9 mm.

The ratios of L/AL, L/W and AL/AW and the widths (W) of shells for each size group (L) are summarized in Table 1 and Figs. 2-5.

Pigmentation of animal

The head region of the specimens of *Bulinus sericinus* was dark (Fig. 6). The mantle had dark grey to black, irregular patches on a greyish background. The tunica propria of the visceral hump was transparent, except for the area overlying the ovotestis, which was pigmented.

Radula

Rachidian teeth: The rachidian teeth (Fig. 8) had 2 cusps. Among the 64 radulae examined, 5 specimens had asymmetrically developed cusps (Fig. 8a), and 11 specimens, which were larger specimens with the shell length greater than 9 mm, had a distinct denticle between the 2 cusps (Fig. 8b).

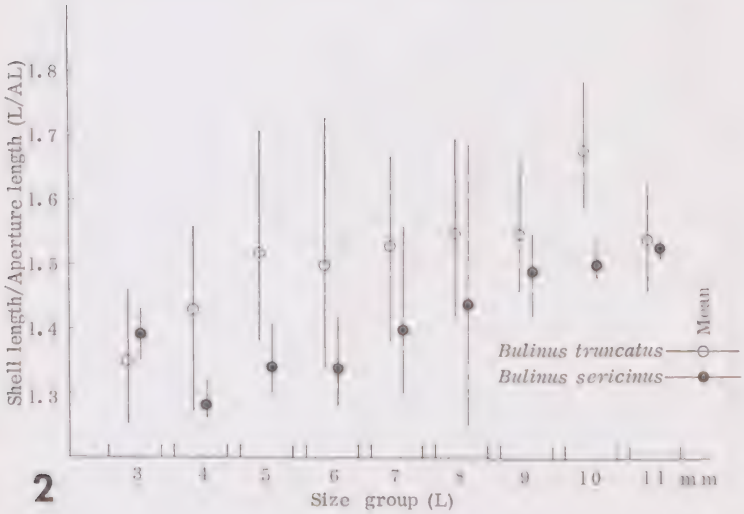
Lateral teeth: The endocones of the 1st lateral teeth were large and had almost the same height as the mesocones beside them. The mesocones of the 1st lateral teeth were large and angular-sided. However, lateral teeth of snails with shells smaller than 5.5 mm length had mesocones with one side angular and the other side evenly rounded. The ectocones of the 1st lateral teeth were triangular in shape and slightly smaller than the adjacent mesocones. Usually a denticle was present between the endo- and the mesocone, and between the meso- and the ectocone. In most cases the endocones of the lateral teeth split into 3, 4, 5 and 6 cusps in the L7, L8, L9 and L10 teeth, respectively. The corrugated or serrated lateral edge of the hook-body was usually noticeable from the L3 or L4 teeth onward.

A scatter diagram of the number of lateral teeth in a half row to the shell length of the animal from which the radula came is shown in Fig. 9.

Reproductive system

The numbers and percentages of euphallic specimens for the 4 samples examined at different times are tabulated as follows.

Date	Number of snails		Euphallic snails %
	Examined	Euphallic	
11/11/70	149	3	2.0
2/09/71	103	2	1.9
5/24/71	71	2	2.8
6/17/71	69	0	0



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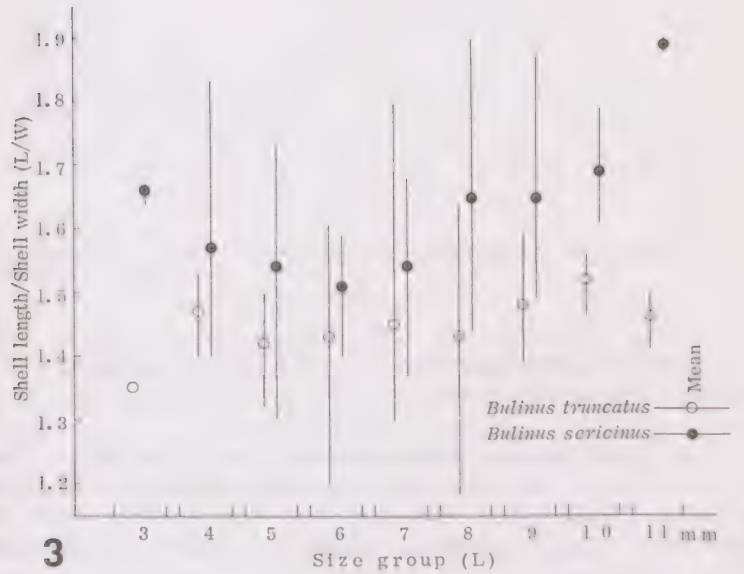

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FIGS. 2, 3. Shell measurement ratios in the different size groups (shell length, L) for *Bulinus sericinus* and *B. truncatus*, showing ranges and means. FIG. 2. Ratios of shell length/aperture length. FIG. 3. Ratios of shell length/shell width. The data on *B. truncatus* are from Wu (1972).

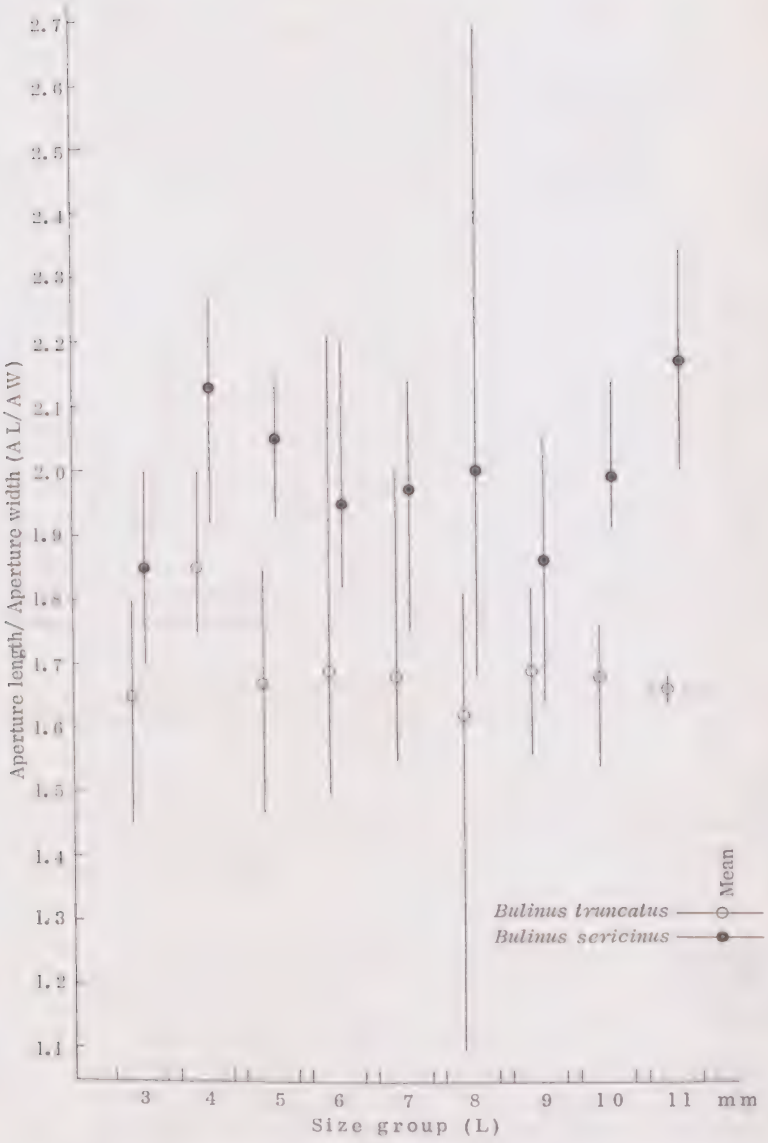


FIG. 4. Ratios of shell aperture length/aperture width for *Bulinus sericinus* and *B. truncatus*. The data on *B. truncatus* are from Wu (1972).

About 2/3 of the aphallic specimens showed a trace of a penial complex, which indicated the formation of the male penial complex during developmental stages, with its subsequent degeneration when the snails reached the 3 mm (shell length) size. In a snail of 4.6 mm shell length, the penial complex had no connection with its vas deferens (Fig. 11a).

Snails of 3 mm shell length (Fig. 10a, b). Aphallic specimen. The ovotestis had no follicular structure; the ovisperm duct was long and smooth, without the seminal vesicle enlargements in its upper half; the primordium of albumen gland could be seen; the uterus complex was a slightly enlarged tube. In the male system, the

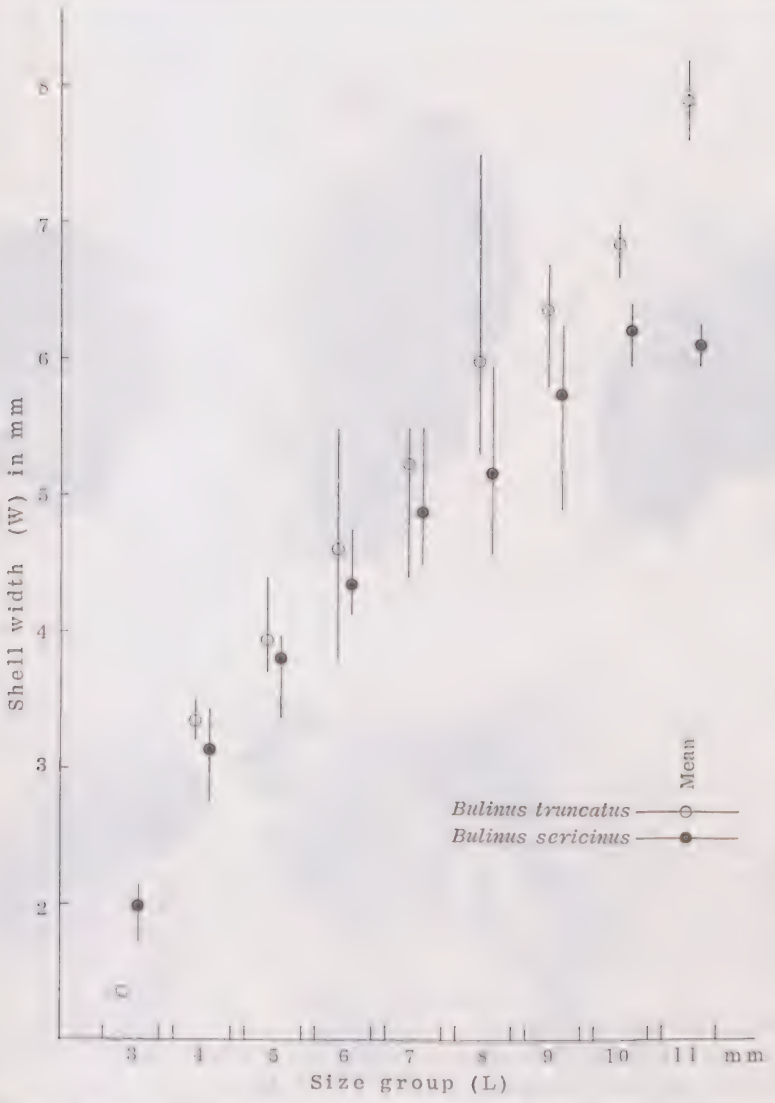
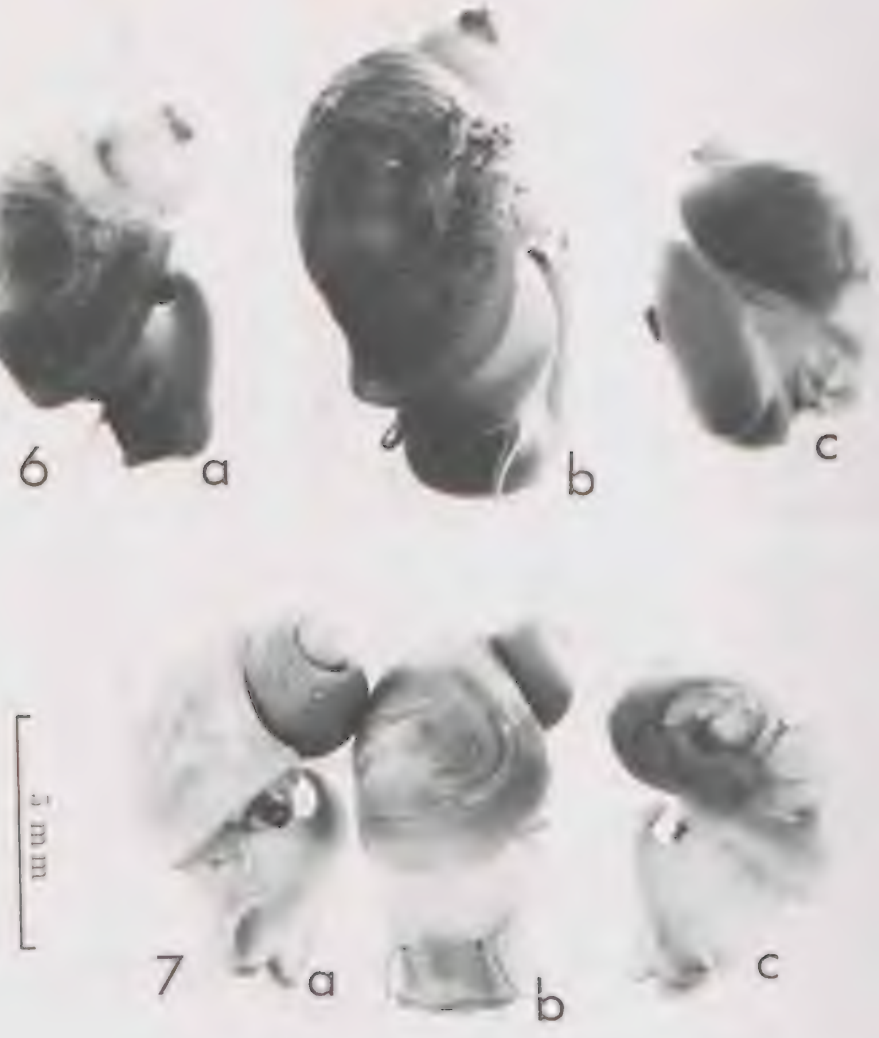


FIG. 5. Shell widths of *Bulinus sericinus* compared with *B. truncatus*. The data on *B. truncatus* are from Wu (1972).

prostate gland and sperm duct were visible, but not the vas deferens.

Snail of 4.6 mm shell length (Fig. 11a, b). Aphallic specimen. The ovotestis already had a differentiated follicular structure; the albumen gland was already lobed; the proximal end of the oviduct was bent to form the oviducal crook; the spermatheca was rod-shaped; the penial complex was extremely enlarged, but separated from the rest of the male system.

Snail of 5.8 mm shell length (Fig. 12a, b). Aphallic specimen. The ovotestis had a follicular structure and the ovisperm duct was smooth; the oviduct was variously bent and the oviducal crook was quite evident; the uterine complex had begun to differentiate into oöthecal and muciparous regions; the male sperm duct had begun to coil; the vas deferens was disconnected, its blind duct terminating at the level of the vagina; the penial complex was degenerate, being merely a small sac behind the left tentacle.



FIGS. 6, 7. Animals with shells removed, showing occurrence of pigmentation: a, left side view; b, dorsal view; c, right side view. FIG. 6. *Bulinus sericinus*. FIG. 7. *B. truncatus*.

Snail of 6.8 mm shell length (Fig. 13a, b). Aphallic specimen. The general structure was the same as that of the 5.8 mm snail, except the seminal vesicle at the upper half of the ovisperm duct was evident, which indicated the onset of maturity at this stage.

Snails of 7.3 and 9 mm shell lengths (Figs. 14-16, a and b). Aphallic specimens (Figs. 14-15, a and b). The general structure was the same as that described previously for *Bulinus truncatus* (Wu, 1972), except that 2/3 of the specimens examined had a non-functional, degenerated, small sac as a trace of the penial complex immediately behind the left tentacle.

Euphallic specimen (Fig. 16a, b). The general structure was the same as that

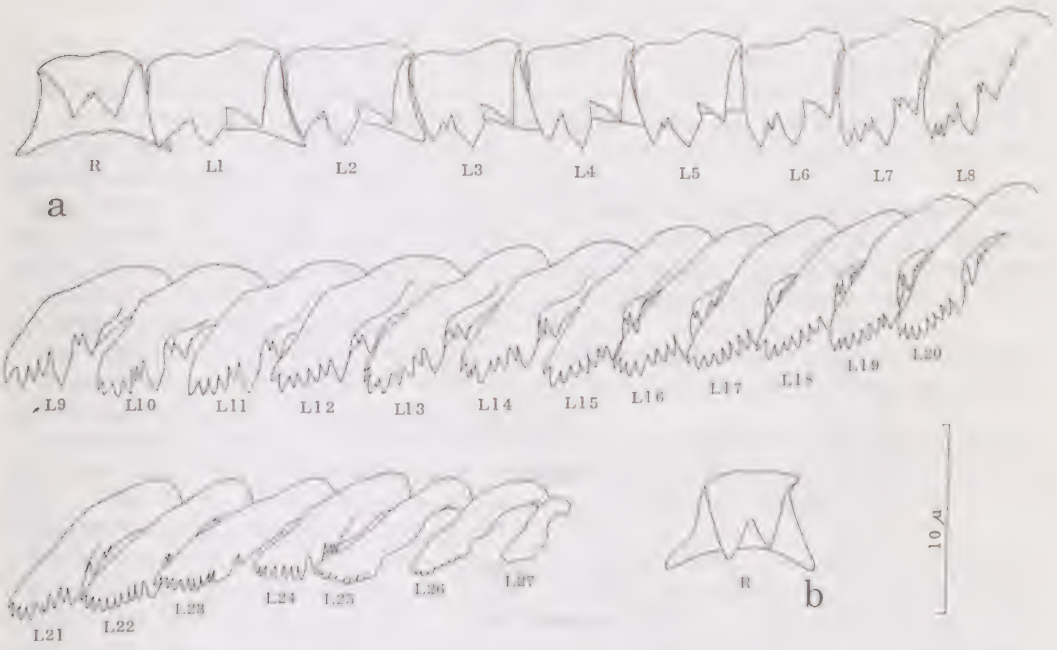


FIG. 8. Radula of *Bulinus sericinus*. a, A half transverse row, dorsal view; R = rachidian tooth; L1, L2, L3 = 1st lateral tooth, 2nd lateral tooth, 3rd lateral tooth, etc. b, Rachidian tooth showing asymmetrically developed cusps.

described previously for *Bulinus truncatus* (Wu, 1972).

Relationships of organ sizes (as measured by their areas in ventral view). The size relationship between the ovotestis and albumen gland during growth were as follows: prior to 7 mm shell size, the ovotestis was slightly larger than the albumen gland; at 7-8 mm shell size, the ovotestis was about the same size as the albumen gland; those specimens with shells larger than 8 mm usually had ovotestes that were smaller than their albumen glands.

During early development of the reproductive system, the prostate gland (P) was initially larger than the spermatheca (Sp) and slightly smaller than the albumen gland (Ag). It became smaller relative to both albumen gland and spermatheca in the aphallic specimens. However, the prostate gland was larger than the spermatheca and was smaller than the albumen gland in the 9 mm euphallic specimen. The relationships between the sizes of the albumen glands and the prostate glands, and the spermathecae and the prostate glands for 6 size groups are tabulated as follows:

Shell size group (in mm)	Euphallic		Aphallic	
	Ag : P	Sp : P	Ag : P	Sp : P
3	.	.	1 : 1	1 : 2
4	.	.	1.5 : 1	1 : 5
5	.	.	1.8 : 1	1 : 5
6	.	.	1.7 : 1	1 : 6
7	.	.	5 : 1	1 : 1
8	2 : 1	1 : 3	8 : 1	1 : 1

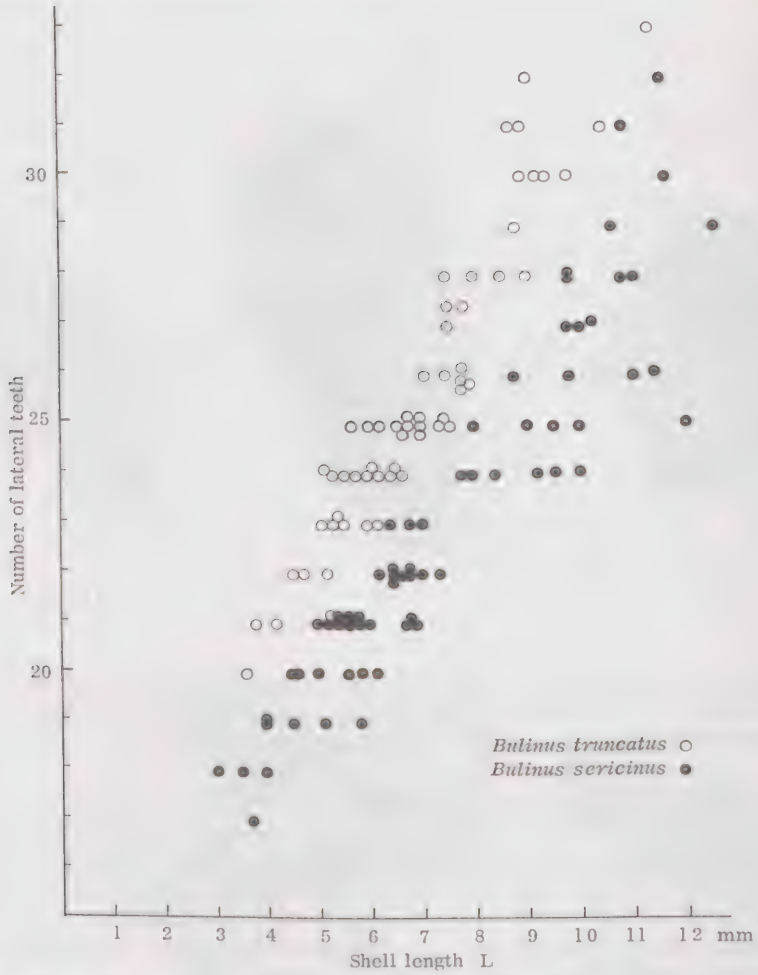


FIG. 9. Number of lateral radular teeth in a half transverse row plotted against shell length for *Bulinus sericinus* and *B. truncatus*. Data on *B. truncatus* are from Wu (1972).

Electrophoresis

The foot muscle esterases of both *Bulinus truncatus* and *B. sericinus* were identical (Fig. 17A-C). Both had a prominent dense band 8 and a fast-running, diffuse band 10. The slow-running, diffuse bands 1, 4, 5 and 6 were only barely visible. R_f values of the esterase bands were as follows: band 1 (0.047 ± 0.011), 4 (0.168 ± 0.006), 5 (0.276 ± 0.010), 6 (0.440 ± 0.015), 8 (0.569 ± 0.007), 9 (0.672 ± 0.016) and 10 (0.804 ± 0.009). (Esterase bands 1, 4, 5, 6, 8, 9 and 10 in this paper correspond to bands 10, 7, 6, 5, 3, 2 and 1, respectively, in Wu, 1972: 135.)

Immunology

Foot muscle antigens of *Bulinus sericinus* tested against antisera for *B. tropicus* produced strong 'non-identity' precipitates between the test-antigen well and the pre-absorbed well of the micro-Ouchterlony double diffusion plate, indicating the presence of non-homologous proteins between the 2 populations. Precipitin bands were not observed when *B. sericinus* antigens were tested against antisera for *B. truncatus*.

COMPARISONS OF *BULINUS SERICINUS* WITH *B. TRUNCATUS*

The mean L/AL ratios of *Bulinus sericinus* for each shell size group (L) were less than those of equivalent *B. truncatus* specimens (Table 1 and Fig. 2), except for the 3 mm size group. The grand mean of L/AL showed that the shells of *B. sericinus* were medium-spired (mean L/AL = 1.39) while those of *B. truncatus* were high-spired (mean L/AL = 1.53) (Table 1).

The mean L/W of *Bulinus sericinus* for each size group (L) were all greater than those of equivalent *B. truncatus* specimens (Table 1 and Fig. 3), and the shell widths (W) of *B. sericinus* for each size group were less than those of comparable *B. truncatus* (Table 1 and Fig. 5). Thus, the shells of *B. sericinus* were narrower and less inflated than *B. truncatus* (Fig. 1).

The mean AL/AW ratios of *Bulinus sericinus* for each size group (L) were greater than those of comparable *B. truncatus* (Table 1 and Fig. 4), reflecting the narrower apertures of *B. sericinus* shells (Fig. 1).

Considerable difference was observed between our topotypes of Ethiopian *Bulinus sericinus* and Egyptian *B. truncatus* in pigmentation of the mantle and tunica propria. The former population was pigmented (Fig. 6a-c) while the latter lacked pigmentation (Fig. 7a-c).

Rachidian cusp deformity in *Bulinus sericinus* (15 out of 64 specimens examined had asymmetrically developed cusps; see Fig. 8a) differed from that of *B. truncatus* (among 150 specimens examined, 23 had 1 cusp missing and 25 had both cusps missing; see Wu, 1972). Similar rachidian tooth deformities in *B. truncatus* have been observed also from other localities (El-Gindy & Rushdi, 1962; Brown, 1965).

The number of lateral teeth in a half row in bulinine radulae is proportional to the shell length (Wu, 1972). Comparison of the above 2 populations demonstrated that the numbers of lateral teeth were greater in *B. truncatus* than in *B. sericinus* with shells of equivalent size. The scatter diagram (Fig. 9) shows that in this respect the ranges do not overlap.

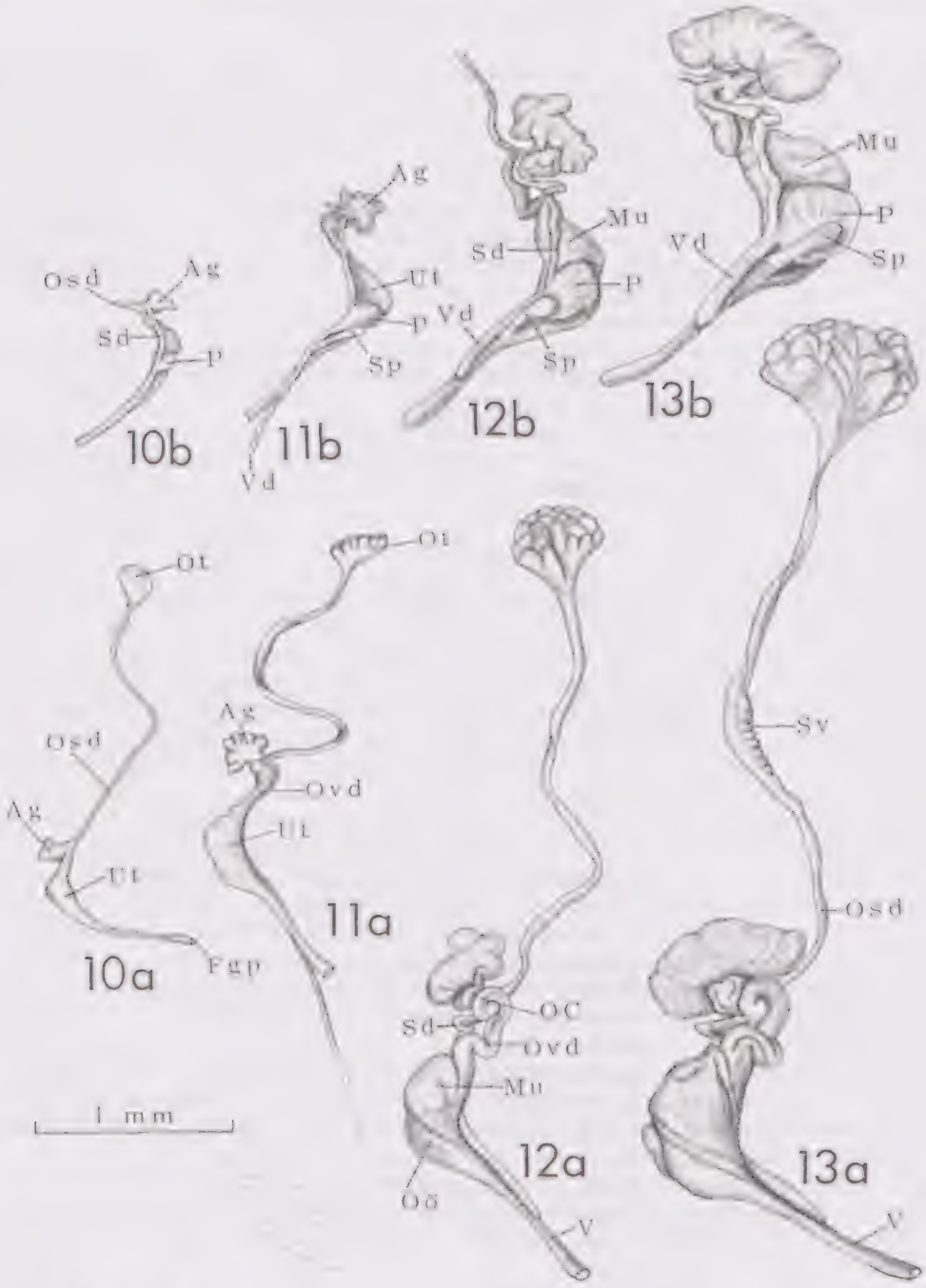
The differences in the reproductive system were (1) the reproductive maturity (using the initial enlargement of the seminal vesicle as an indicator) occurred at 6.8-7.0 mm shell length in *Bulinus sericinus* and at 4.6-5.0 mm shell length in *B. truncatus*, and (2) the percentage of euphallic individuals was low (1.8%) for *B. sericinus*, while it was found to be relatively higher (15.2%) for *B. truncatus* in a previous study from our laboratory (Wu, 1972).

There were no differences detected between *Bulinus sericinus* and *B. truncatus* in electrophoretically separated esterases (Fig. 17) from foot muscle, or in antigen-antibody reactions of foot muscle tissues.

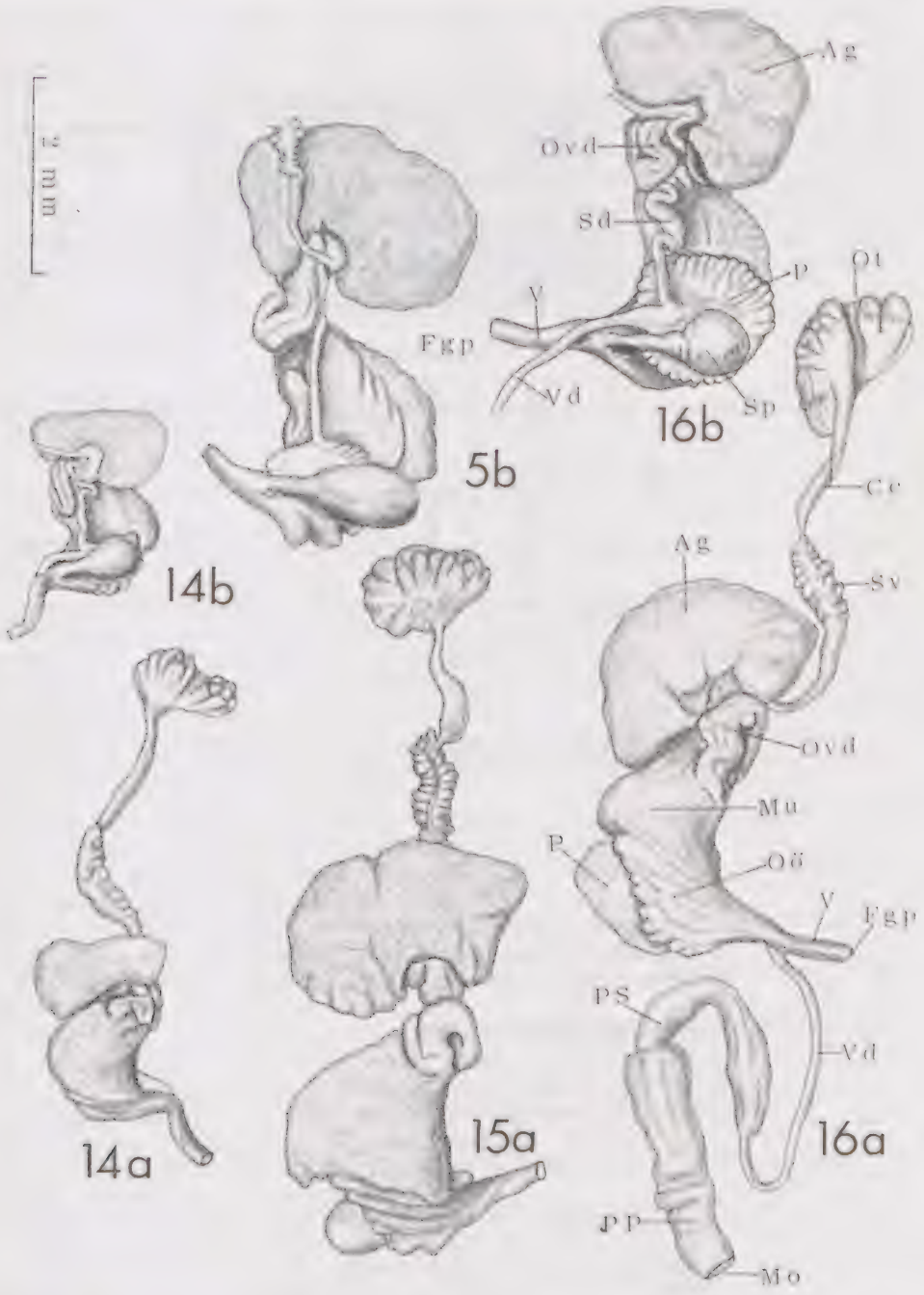
In regard to schistosome susceptibility, 52.6% of the 50 *Bulinus sericinus* exposed to an Egyptian strain of *S. haematobium* were infected (Wu & Burch, 1974). Only 3% of the specimens of Egyptian *B. truncatus* exposed by Lo (1972) to the same parasite strain were infected.

Wu's (1972) attempts to mate *Bulinus sericinus* with a diploid albino strain of *B. tropicus* succeeded in producing vigorous but sterile F_1 progeny in 1 of 3 experiments, while none of the matings of *B. truncatus* with the same albino strain succeeded in producing F_1 progeny.

In general, the morphology of *Bulinus sericinus* was found to be the same as that of *B. truncatus*. However, differences, in some cases rather minor, were found in shell morphology, external body pigmentation, the degree of rachidian tooth deformity, the number of lateral teeth in a transverse half row, the percentage of aphallic animals and the degree of susceptibility to an Egyptian strain of *Schistosoma haematobium*. These are undoubtedly due to genetic differences between the



FIGS. 10-16. The reproductive system of *Bulinus sericinus* at different stages of growth as measured by shell lengths. FIG. 10. Shell length (L) = 3 mm. FIG. 11. L = 4.6 mm. FIG. 12. L = 5.8 mm. FIG. 13. L = 6.8 mm. FIG. 14. L = 7.3 mm. FIGS. 15, 16. L = 9 mm. a, dorsal views; b, ventral views. Ag = albumen gland; Cc = collecting canal of



ovotestis; Fgp = female genital pore; Mo = male opening; Mu = muciparous gland of uterus; OC = oviducal crook; Oö = oöthecal gland of uterus; Osd = ovisperm duct; Ot = ovotestis; Ovd = oviduct; P = prostate gland; PP = preputium; PS = penial sheath; Sd = sperm duct; Sp = spermatheca; Sv = seminal vesicle; Ut = uterus; V = vagina; Vd = vas deferens.

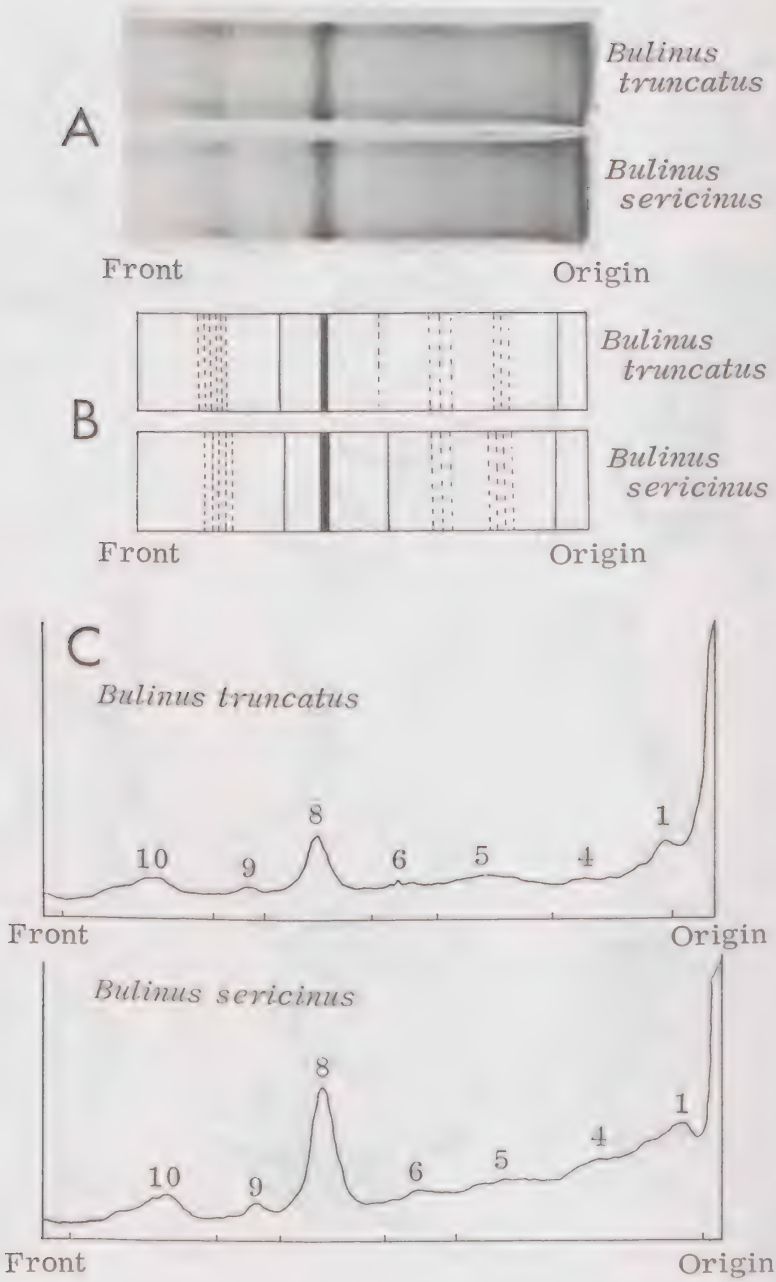


FIG. 17. Electrophoretically separated foot muscle esterases of adult *Bulinus truncatus* and *B. sericinus*. A, photographs of stained gel columns; B, drawings of the gels; C, densitometric tracing.

populations, but the magnitude of these differences do not seem great enough to unequivocally assign separate species status to the 2 populations, unless it is found that significant reproductive barriers exist which prevent interbreeding between the 2 forms. This latter aspect has not yet been investigated. Brown & Wright (1972) concluded that all Ethiopian tetraploid populations are *Bulinus truncatus* because of similarity to Egyptian snails in morphology and egg proteins and the susceptibility of some tetraploid Ethiopian snails to infection with Egyptian *Schistosoma haematobium*. However, for the present, it might be well to consider tetraploid bulinines from the Ethiopian highlands answering to the description of topotype material as a distinct race in order to recognize its differences from typical *B. truncatus*.

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ALLOZYME VARIATION AND GENIC HETEROZYGOSITY IN THE BAHAMAN PULMONATE SNAIL *CERION BENDALLI*[1, 2]

David S. Woodruff

ABSTRACT

Studies of electrophoretically demonstrable variation in 21 enzymes and 1 non-enzymatic protein in a population of the land snail *Cerion bendalli* from Great Abaco island revealed that this species is polymorphic at 23% of the loci surveyed and that individuals are heterozygous at about 7% of their structural gene loci. Variable allozymes include malate dehydrogenase, phosphoglucose isomerase, glutamic oxalacetic transaminase, leucine aminopeptidase and a nonspecific esterase. Observed segregation frequencies for these diallelic systems are in close agreement with Hardy-Weinberg expectations and indicate that this facultative hermaphrodite is outbreeding. Slightly lower levels of genic heterozygosity occur in samples from 2 small cays immediately offshore, but the genetic distances (D) between these 3 populations are negligibly small.

The recent introduction of complex quantitative methods of character analysis and techniques from biochemistry has had a beneficial influence on systematics (Selander, 1971; Gould & Johnson, 1972). This is especially true for taxonomically difficult groups like the terrestrial pulmonates of the genus *Cerion* which have been proven almost impossible to classify in terms of conventional categories (Mayr & Rosen, 1956; Clench, 1957). The evolutionary problems posed by these remarkably variable West Indian snails have also remained unresolved despite the efforts of numerous workers (Plate, 1906, 1907; Bartsch, 1920; Mayr, 1963). Now, as a result of an approach combining the newer techniques for the analysis of genetic and phenetic variation, S. J. Gould and I are successfully confronting the important systematic and evolutionary problems presented by the more than 600 "species" of this group (Woodruff, 1975). Initial work by Gould (1969, 1971) demonstrated the power of multivariate biometric analyses of the variation in shell morphology. Here, I report the first attempts to elucidate the genetic basis underlying the extraordinary phenetic variation. In this paper I describe the electrophoretic procedures used to study allelic variation of structural genes producing soluble enzymes. The techniques and patterns described will provide a basis for subsequent discussions of the biochemical systematics and evolutionary biogeography of these snails.

Although Clench (1957) lists 9 "species" of *Cerion* from the islands of the Little Bahama Bank, extensive field collecting during the last 2 years indicates that only 2 taxa are present (Gould & Woodruff, in prep.). *C. bendalli* occurs on Grand Bahama, Little Abaco and Great Abaco islands in the northern Bahamas (Clench, 1938). The species was described by Pilsbry & Vanatta (1896) from Great Abaco. It has a relatively narrow, ribless or fine-ribbed shell and is mottled with patches

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[1]This study is fifth in a series of papers on The Natural History of *Cerion*. Other studies are Gould (1969, 1971), Gould, Woodruff & Martin (1975) and Woodruff (1975).

[2]Supported (in part) by N. S. F. Grant GB 35235 to S. J. Gould and grants from the Clark and Milton Funds of Harvard University.

of brown and white. Field work has established that its geographic range is essentially allopatric to that of the only other species occurring in these islands: *C. abacoense* Pilsbry & Vanatta, 1895. In southern Great Abaco these 2 taxa meet in a narrow zone of allopatric hybridization (*sensu* Woodruff, 1973). The populations described here lie 20 km north of this zone and well within the general range of *C. bendalli*.

MATERIALS AND METHODS

Three samples of adults were collected on September 16, 1972 from an area on the east coast of Great Abaco 10 km south of Marsh Harbour. At this point a narrow causeway connects the mainland with the Bahamas Agricultural Industries Ltd. dock on Snake Cay immediately offshore. The causeway, built in the early 1960's, traverses shallow mangrove flats and Tuggy Cay, which lies between Snake Cay and the mainland. Populations were sampled on Snake Cay, Tuggy Cay and the adjacent mainland. The 3 localities are about 400 m apart. Density was high at each site, with 10 or more adults occurring per m^2 of low vegetation.

Snails were collected and transported dry, in plastic bags, to the laboratory. They were fed damp filter paper until they had egested all natural foodstuffs. They were then induced to estivate and held dry, without further maintenance, until required for biochemical analysis. While most electrophoretic analyses were performed within 3 months of collection, enzyme activity and band resolution was still satisfactory in animals that had estivated for 9 months.

Prior to the preparation of enzyme extracts, activity was induced by placing estivating snails in trays of water. As the shells were required for biometric studies, it was necessary to remove the animals without damaging their shells. This proved difficult, at first, as healthy snails withdrew 2-3 whorls back from the aperture at the slightest disturbance. Successful extraction of over 80% of the snails in each sample was eventually achieved by placing them in a 1% solution of propylene phenoxytol as suggested by Owen (1955) and Turner (1960).

Following snail extraction, the cephalopodal mass was separated from the rest of the body and minced finely on a cold glass plate. The resulting slurry was transferred to a centrifuge tube and agitated with 2 volumes of distilled water. The tubes were incubated at room temperature for 10-15 minutes and then centrifuged at 25,000 g for 30 minutes at 2°C. The supernatant was removed and electrophoresed directly.

Electrophoresis was performed on horizontal starch gel slabs following the techniques of Selander et al. (1971). Electrostarch Lot 146 (Otto Hiller, Madison, Wisconsin) was used throughout this study. Seven buffer systems were employed to determine the optimum technique for each enzyme system. Following electrophoresis, each slab was cut into 3 or 4 slices and these were stained for various enzymes. Again, protein staining techniques are described by Selander et al. (1971). Biochemical variation in 16 enzymes and general protein was studied. Eighteen individual snail samples were analyzed on each gel and activity patterns were scored immediately and photographed. Each snail was scored for all enzymes studied wherever possible. Sample sizes for the 3 populations were: mainland, 97; Tuggy Cay, 42; Snake Cay, 41.

The variation described below is essentially phenotypic variation. Although genetic interpretation will be offered in some cases, it should be stressed that formal genetic crosses have not yet been undertaken. The tentative genetic interpretations are based on 2 criteria. First, patterns of banding of particular enzymes correspond to simple models of molecular structure. In most cases the inferred structures are similar to those of functionally analagous enzymes in other animals whose structure has been established by other techniques. Second, phenotypic ratios were found to agree closely with Hardy-Weinberg expectations for large outbreeding populations.

In the following account, independent zones or bands of enzymatic activity are numbered sequentially from the most anodal to the most cathodal. In polymorphic systems, alleles are

labelled a, b, c . . . in order of decreasing electrophoretic mobility. The allelic interpretations and numbering systems accomodate all the variation detected to date in over 2000 snails from Curacao, Puerto Rico, Great Inagua, New Providence, Grand Bahama, Great Abaco and Little Abaco, and not just the variation in the 3 samples described here. Unless noted, all enzymes migrated towards the anode.

When biometric analyses are completed, the shells of the animals involved in this report will be deposited in the collection of the Museum of Comparative Zoology, Harvard University. They may be identified by the author's field numbers: 243 (mainland), 245 (Tuggy Cay) and 244 (Snake Cay).

RESULTS

Esterases (continuous tris-citrate I buffer, 140 volts, 4 hours). Activity was studied using 3 esters (α-naphthyl acetate, α-naphthyl proprionate, and indoxyl acetate) and an inhibitor (eserine sulfate). Routine analysis was performed with α-naphthyl acetate. Seven zones of nonspecific esterase activity are recognized. Est-1 appears as a single well-defined band on all 3 substrates. No variation was detected in its mobility. Est-2 is a variable enzyme; interpretable as a codominant diallelic system with 2 banded heterozygotes. On the basis of the study of this enzyme in other *Cerion*, these alleles are designated Est-2^b and Est-2^c (Fig. 1). Esterase-2^c is fixed in the 2 offshore populations and almost fixed on the mainland (Table 1). Activity presently referred to Est-3 and Est-4 develops as a series of variable bands and subbands and no genetic interpretation is yet possible. These bands do not appear when indoxyl acetate is used as the substrate. Est-5 develops as a broad diffuse band of variable mobility; its resolution is unsatisfactory on the systems employed. Est-6 appears as a single, sharp band close to the origin. Mobility is identical in all snails studied. Activity was inhibited by 10^{-3}M eserine. Est-7 migrated cathodally under these conditions and develops as a single well-defined band. It is monomorphic in these populations but varies in mobility in other *Cerion*.

Alcohol dehydrogenase (Tris-versene borate, 200 v, 5 hrs). A single very faint

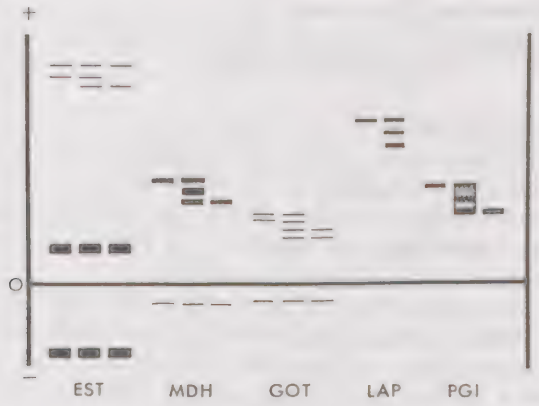

FIG. 1. Schematic diagram of variation in allozyme patterns of individual *Cerion bendalli*. Patterns shown as Esterase-1, Est-2 ($2^b/2^b$, $2^b/2^c$, $2^c/2^c$), Est-6, Est-7; Malate dehydrogenase-1 ($1^a/1^a$, $1^a/1^b$, $1^b/1^b$), MDH-2; Glutamic oxalacetic transaminase-1 ($1^a/1^a$, $1^a/1^b$, $1^b/1^b$), GOT-2; Leucine aminopeptidase-1 ($1^a/1^a$, $1^a/1^b$); Phosphoglucose isomerase-1 ($1^a/1^a$, $1^a/1^b$, $1^b/1^b$).

band was resolved in 18 freshly homogenized samples from the mainland population. It migrated anodally with a mobility of 0.60 compared to indophenol oxidase. All activity was lost in samples that were frozen or stored more than a few hours. As a single band of identical mobility was detected in *Cerion bendalli* from northern Great Abaco and Grand Bahama, it is tentatively concluded that this species is homozygous for ADH-1.

α-Glycerophosphate dehydrogenase (Tris-maleate, 100 v, 5 hrs). A single weak band migrating with a mobility of about 1.20 relative to indophenol oxidase was detected in fresh homogenates. No variation was found and the enzyme is tentatively described as monomorphic α-GPD-1.

Isocitrate dehydrogenase (continuous tris-citrate I, 140 v, 4 hrs or Tris-maleate, 100 v, 5 hrs). Two zones of weak activity were located using fresh, never frozen homogenates. IDH-1 was monomorphic and resolved as a single narrow band with a mobility of 1.15 relative to indophenol oxidase. IDH-2 was also invariant: developing as 2 narrow bands with relative mobilities of 0.42 and 0.47 with respect to IPO.

Lactic dehydrogenase. No activity was found even in fresh, never frozen samples. The detection of this enzyme has been sporadic in molluscs (Manwell & Baker, 1970).

Malate dehydrogenase (Tris-maleate, 70 v, 20 hrs). Two NAD-dependent enzymes were detected. MDH-1 migrates anodally and is apparently a dimer, heterozygotes having 3 bands (Fig. 1). The frequency of the fast allele MDH-1^a ranged from 0.28-0.37 in the 3 samples (Table 1). MDH-2 is also polymorphic in *Cerion bendalli* but only a single allele MDH-2^b was found in these populations. It migrates cathodally as a single band.

6-*Phosphogluconate dehydrogenase* (continuous tris-citrate I, 140 v, 4 hrs). Only a single anodal band was detected in these samples. Elsewhere in the range of *Cerion bendalli*, however, homogygotes for a slower allele and 3-banded heterozygotes have been identified.

Sorbital dehydrogenase and *xanthine dehydrogenase*. Although activity referable to these enzymes has been detected, it is presently uninterpretable.

Indophenol oxidase (continuous tris-citrate I, 140 v, 4 hrs, stained for IDH). A single well-defined band migrates towards the anode. No variation in mobility was detected in samples of *Cerion bendalli;* some variation has been found in other *Cerion*. These populations are tentatively scored as being monomorphic for the allele IPO-1.

Phosphoglucomutase (continuous tris-citrate I, 140 v, 4 hrs). A pattern of 3 anodally migrating bands was revealed in all specimens. There is a single fast band and a slower set of 2 or 3 bands of variable activity. No variation was seen in either system in the samples studied. While the genetic basis of these patterns is not yet clear, the 2 systems are identified as PGM-1 and PGM-2. Elsewhere in the Bahamas variants of PGM-2 have been found.

Phosphoglucose isomerase (Tris-maleate, 70 v, 20 hrs). Resolution of this enzyme is poor on the systems employed; streaking rendered many samples unscorable. The pattern is variable and appears to involve either a single fast band, a single slow band, or a smear encompassing the positions of both bands (Fig. 1). Frequency of the fast allele PGI-1^a was 0.39 in the mainland sample; reliable estimates are not available for the 2 island populations.

Glutamic oxalacetic transaminase (Tris-maleate, 70 v, 20 hrs or Lithium hydroxide, 300 v, 4 hrs). Two polymorphic enzymes were detected. GOT-1 develops as a diallelic allozyme: fast and slow homozygotes are represented by well-defined doublet bands, the heterozygotes by 4 bands (Fig. 1). The 2 alleles are equally

TABLE 1. Phenotypic (and presumed genotypic) proportions and allele frequencies for polymorphic loci in 3 populations of *Cerion bendalli*. The 3 populations are the mainland (M), Tuggy Cay (T) and Snake Cay (S). Enzymes are esterase-2 (Est-2), malate dehydrogenase-1 (MDH-1), phosphoglucose isomerase-1 (PGI-1), glutamic oxalacetic transaminase-1 (GOT-1) and leucine aminopeptidase-1 (LAP-1).

Enzyme	Sample	N	Observed (expected)			Allele frequency	
			$2^b/2^b$	$2^b/2^c$	$2^c/2^c$	Est-2^b	Est-2^c
Est-1	M	89	1(0.2)	6(7.6)	82(81.2)	0.04	0.96
	T	41	-	-	41(41)	0.00	1.00
	S	41	-	-	41(41)	0.00	1.00
			$1^a/1^a$	$1^a/1^b$	$1^b/1^b$	MDH-1^a	MDH-1^b
MDH-1	M	89	8(6.7)	33(35.5)	48(46.7)	0.28	0.72
	T	41	3(3.5)	18(17.0)	20(20.5)	0.29	0.71
	S	41	6(5.5)	18(19.0)	17(16.5)	0.38	0.62
			$1^a/1^a$	$1^a/1^b$	$1^b/1^b$	PGI-1^a	PGI-1^b
PGI-1	M	60	8(9.2)	31(28.6)	21(22.2)	0.39	0.61
			$1^a/1^a$	$1^a/1^b$	$1^b/1^b$	GOT-1^a	GOT-1^b
GOT-1	M	97	23(20.8)	44(48.3)	30(27.9)	0.46	0.54
	T	41	13(12.3)	19(20.3)	9(8.4)	0.55	0.45
	S	41	12(11.3)	19(20.5)	10(9.3)	0.52	0.48
			$1^a/1^a$	$1^a/1^b$	$1^b/1^b$	LAP-1^a	LAP-1^b
LAP-1	M	97	77(78.0)	20(17.9)	0(1.0)	0.90	0.10
	T	42	34(34.4)	8(7.2)	0(0.4)	0.90	0.10
	S	41	37(37.1)	4(3.8)	0(0.1)	0.95	0.05

abundant in these populations (Table 1). GOT-2 remains close to the origin, and on the lithium hydroxide buffer it migrates cathodally. Activity is weak but a single band of identical mobility was found in all individuals.

Leucine aminopeptidase (continuous tris-citrate I, 140 v, 4 hrs). Two forms of this enzyme were detected: a single fast band and a 3-banded pattern (Fig. 1). As *Cerion* with a single slow band have been found elsewhere, these are interpreted as LAP-1^a homozygotes and LAP-1^a/LAP-1^b heterozygotes. In these samples the frequency of LAP-1^a ranged from 0.90-0.95 (Table 1).

Acid phosphatases (Tris-maleate, 70 v, 20 hrs). Two zones of activity were detected. ACP-1 develops as a poorly defined band of considerable activity. Although streaking is a major problem with this enzyme, no significant variation was detected in the mobility of this band in *Cerion bendalli*. ACP-2 appears as a well-defined band close to the origin; its mobility was invariant. Both enzymes appear to be more variable in *Cerion* from elsewhere.

Alkaline phosphatase (Lithium hydroxide, 300 v, 4 hrs or Tris-EDTA-borate (Rock U) pH 9.0, 200 v, 5 hrs). Two zones of activity were resolved. The more mobile AP-1 developed as a single band of high activity and is apparently monomorphic in *Cerion bendalli*. Satisfactory resolution of the 2nd zone AP-B was not achieved with any of the buffers employed. Typically, it would develop as a smear of variable intensity extending from the origin halfway to the position of AP-1.

General proteins (Tris-maleate, 70 v, 20 hrs, stained with amido black). Several zones of weak activity were detected. Variation is uninterpretable except in the case of PT-B, which developed as a single well-defined band of uniform mobility in the samples studied. It does not clearly correspond in mobility to any of the enzymes described above.

DISCUSSION

Tentative genetic interpretations are offered for 22 of the proteins surveyed. Polymorphic variation was detected in 5 enzymes: Est-2, MDH-1, PGI-1, GOT-1 and LAP-1. Variation in each case is understandable in terms of simple Mendelian systems involving pairs of codominant alleles. Phenotypic ratios (and presumed genotypic ratios) agree closely with Hardy-Weinberg expectations for large outbreeding populations (Table 1). These 5 loci segregate independently, and this is quite reasonable as one species of *Cerion* is known to have 27 pairs of chromosomes (Burch & Kim, 1962).

The mainland population was found to be polymorphic at 22.73% of the 22 loci. By direct counting, an average heterozygosity per individual of 6.86% was estimated. In order to compare this population with the other 2, it is necessary to ignore the variation in PGI-1; when this is done these values decrease to 19.05% and 5.44% respectively. Tuggy Cay and Snake Cay populations were both polymorphic at 14.29% of the remaining 21 loci. Average heterozygosity per individual was 4.82% in the Tuggy Cay sample and 4.80% on Snake Cay. The reduction in heterozygosity in the offshore populations is due to the presence of the rare Est-2^b allele in 8% of the mainland sample.

In connection with the interpretation of these results, it must be stressed that these are minimum estimates since they are based on only those gene substitutions that are detectable electrophoretically. For many enzymes we know that true levels of genic variability may be 3 times as high (Lewontin, 1974). For this reason no special significance is attached at this time to the slightly lower levels of heterogeneity in the cay samples, although such reduced variation in insular populations is predicted by present evolutionary theory and has been documented in several animals (Selander et al., 1971; Webster, Selander & Yang, 1973).

Genetically (on the basis of 21 allozymes) these 3 populations are almost indistinguishable from one another. The normalized identity of genes (I of Nei, 1972) between the 3 pairwise combinations of these samples were in the range 0.9991-0.9995. Accordingly, the values of Nei's (1972) genetic distance (D) were extremely small: 0.0005-0.0009. A replicated goodness of fit (G-statistic) test indicates a high degree of probability that the observed differences in allelic frequencies are due to sampling error. Today these 3 populations of *Cerion bendalli* are isolated from one another by narrow (100-400 m) water gaps. The observed genetic similarity between the 3 samples suggests that cay colonies were not founded by single individuals but rather by larger propagules whose variation encompassed that of the ancestral population. This is interesting because the prevailing view has been that isolated colonies of *Cerion* are founded by single waifs moved in haphazard fashion by hurricanes. Such a process has been invoked to explain the crazy-quilt pattern of distribution of *Cerion* morphotypes or "species" (Mayr, 1963). In the present case, only slight morphological differentiation has occurred between these cay populations and the mainland ones (or for that matter those on Elbow Cay, 7 km further offshore) (Gould & Woodruff, in prep.).

Elsewhere I will describe allozyme variation in 12 populations of *Cerion bendalli* from the northern end of Great Abaco, some 50 km NW of Snake Cay (Gould, Woodruff & Martin, 1975). In these populations Est-2^c is fixed, MDH-2^a occurs at low

frequency, and allele frequencies at the MDH-1, GOT-1 and LAP-1 loci are very similar to those seen in the 3 populations described here. Genetic distance values between populations in these 2 areas are about the same as those calculated between adjacent populations. Electrophoretic surveys of another 22 populations from elsewhere on Great Abaco, from Little Abaco and Grand Bahama have also been completed. While the overall pattern of geographic variation in *C. bendalli* will be described in another paper (Woodruff, in prep.), the available data indicate that the populations described here are typical of the species with respect to levels of genic heterozygosity.

Comparable studies of natural populations of other terrestrial pulmonates are regretably few (Michelson, 1973). Recently, however, Selander & Kaufman (1973b) have reported that in *Helix aspersa*, *Mesodon roemeri* and *Rabdotus mooreanus* a study of 17 loci indicated an average genic heterozygosity per population of 20.7% (range 14-25%). These values are very similar to those reported here for *Cerion bendalli*. The maintenance of genic heterozygosity at these levels necessitates an outbreeding mating system. Thus, *Cerion*, an hermaphrodite (Richter, 1926; Jaenicke, 1933), is apparently an obligate outcrosser like most other pulmonates (Purchon, 1968). In marked contrast, Selander & Kaufman (1973a) found virtually no genetic variation in U.S. populations of the self-fertilizing *Rumina decollata*. Other surveys of allozyme variation involving smaller numbers of individuals and fewer alleged loci have involved *Cepaea hortensis* and *C. nemoralis* (Manwell & Baker, 1968, 1970; Levan & Fredga, 1972; Oxford, 1973, in press), *Arantia arbustorum* (Levan & Fredga, 1972), *Partula* sp. (Schwabl & Murray, 1970) and *Helix pomatia* (Wahren & Tegelstrom, 1973). As with other animals (Selander & Johnson, 1973; Lewontin, 1974), it appears that these land snails are very variable genetically. The study of the local organization and geographic patterns of this rich variation promises to be of major utility in systematically difficult groups like *Cerion*. Even in northern Great Abaco where marked morphological variation occurs in *C. bendalli*, its genetic basis remains undetected (Gould, Woodruff & Martin, 1975). In subsequent contributions we will use this relatively conservative genic variation in our analyses of the extreme phenetic variation seen in these enigmatic land snails.

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I thank Margaret Wu for her excellent assistance in the laboratory. I am indebted to S.J. Gould for support and assistance in the field and to T. Preston Webster, R.K. Selander and Ruth Turner for advice on biochemical problems. This work was carried out at the Biological Laboratories, Harvard University.

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ACCUMULATION OF GALACTOGEN IN THE ALBUMEN GLAND OF *TRIODOPSIS MULTILINEATA* (PULMONATA: STYLOMMATOPHORA) AFTER DORMANCY[1]

Paul H. Rudolph

ABSTRACT

Histochemical and biochemical analyses were undertaken on the carbohydrate content of the albumen gland of *Triodopsis multilineata* from dormancy to 42 days postdormancy. Galactogen is the main carbohydrate secretion product of the albumen gland and is present in dormant as well as active animals. The carbohydrate content rises from a dormant value of 20.5% to a high of 46.6% of the dry weight of the albumen gland on the 24th day postdormancy, with the main increase occurring between the 6th and 12th day postdormancy. Galactogen completely fills all cells of the gland after 30 days postdormancy. The albumen gland appears to become hydrated during the first 6 days following dormancy, during which time there is little change in the carbohydrate content.

The albumen gland of pulmonate molluscs is that portion of the reproductive system which provides the perivitelline fluid for the eggs. The main carbohydrate component of the albumen gland and perivitelline fluid is galactogen, a galactose polymer, which, in pulmonates, is found only in the albumen gland and eggs (e.g., May, 1934; Goudsmit, 1972).

Many terrestrial pulmonates pass the winter in a dormant state and become active with the resumption of favorable conditions in the spring. During the period which follows dormancy, the reproductive system becomes prepared for egg laying. This preparation includes the formation of the perivitelline fluid in the albumen gland. May (1934) has shown that the galactogen content of the albumen gland of *Helix pomatia* Linnaeus rises after winter dormancy and remains high until eggs have been laid. Berrie (1966) has shown that the albumen gland of the basommatophoran *Lymnaea stagnalis* (Linnaeus) changes rapidly in size (volume) on a seasonal basis. Little is known concerning the time required for the accumulation of the galactogen subsequent to winter dormancy in terrestrial pulmonates. This study was undertaken to confirm the presence of galactogen in *Triodopsis multilineata* (Say) and to determine the time required for galactogen accumulation in the albumen gland.

MATERIALS AND METHODS

Active *Triodopsis multilineata* were collected September 14, 1970, from Louisville, Nebraska, U.S.A. The snails were moved to the laboratory the same day and placed in a refrigerator at 4°C in constant darkness to induce dormancy. The snails were removed from the refrigerator 2 months later and placed in plastic boxes with a potting soil-vermiculate-peat moss substrate, at 22°C under constant, diffuse light. The snails were allowed a continuous supply of lettuce throughout the experimental period, which lasted 42 days.

Sampling was done every 6 days. On Day 0, animals were dormant and were analyzed the

[1] From a thesis submitted in partial fulfillment of the requirements for the Master of Science degree at the University of Nebraska.

same day that the remaining animals were allowed to become active. Weight and carbohydrate analyses were performed on 6 samples each test day. Each sample was composed of 4 snails, pooled and analyzed as 1 sample. Histochemical and histological analyses were performed on 3 animals each test day.

Wet and dry weights of the albumen gland were determined to 0.1 mg. Drying was done at 95°C to 100°C for 24 hours (Giese, 1967). Dried albumen glands were finely ground with a rounded glass rod. Lipids were removed to prevent interference with the carbohydrate determinations by 2 successive extractions with chloroform–methanol (2:1 parts by volume). The residue remaining after lipid extraction was placed in 5% trichloracetic acid (TCA) and heated for 15 minutes to remove the carbohydrates (Giese, 1967). The TCA extraction was repeated twice and pooled for carbohydrate estimation. Carbohydrates were estimated by the phenol-sulfuric acid method of Dubois et al. (1956), using galactose as standard. All determinations were done in duplicate. The total animal was dried as above after removing the albumen gland and shell. The dry weight of the albumen gland was added to the dry weight of the total animal without albumen gland to give the total animal dry weight.

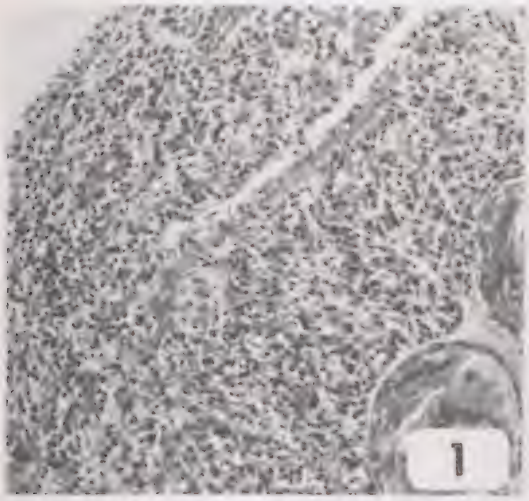
Albumen glands for histological and histochemical preparations were routinely fixed according to Grainger & Shillitoe (1952) and paraffin sections cut at 6 μ. Good sections were obtained from glands which contained a large amount of secretion product by painting the face of the paraffin block with water prior to each section. Lillie's Allochrome (Lillie, 1965) was used as a general morphological stain. Glycogen and galactogen were detected and differentiated by the methods recommended by Grainger & Shillitoe (1952) which consist of: Periodic Acid-Schiff (PAS) (Pearse, 1968), PAS with diastase digestion and parallel control sections (Culling, 1963), PAS with pectinase digestion and parallel control sections (Lillie, 1965), Best's Carmine and aqueous Toluidine Blue (Pearse, 1968) and iodine (Culling, 1963). Malt diastase and pectinase were purchased from the Sigma Chemical Company, St. Louis, Missouri.

RESULTS AND DISCUSSION

The albumen gland of *Triodopsis multilineata* consists of tubules radiating around a central ciliated duct. The tubules are composed of large secretory cells surrounding a central lumen. There are small cells interspersed among the large cells, which may correspond to the centrotubular cells described by a number of workers, including Cavalié & Beylot (1902) and Nieland & Goudsmit (1969) for *Helix pomatia*. The gland is essentially similar to glands described for other pulmonates.

PAS-positive material is present in glands from both active and dormant animals. The PAS-positive material is composed of large, deep red staining granules surrounded by light red staining, homogeneous appearing material. The light red material is removed by diastase digestion prior to PAS treatment. Lability to diastase suggests that the light red PAS-positive material is glycogen. This diastase labile material is present in detectable amounts in glands from Day 0 through Day 24 animals, although a small amount may be present in Day 30 animals. Glycogen has been found in the albumen gland of other pulmonates (e.g., Grainger & Shillitoe, 1952; McMahon et al., 1957; Kugler, 1965; Meenakshi & Scheer, 1968;

FIGS. 1–5. Accumulation of galactogen in the albumen gland of *Triodopsis multilineata* following dormancy. FIG. 1. Day 0 (dormant). The gland contains no galactogen. Dark bodies are nuclei (Lillie's Allochrome). FIG. 2. Day 0 (dormant). Galactogen is concentrated in the region of the central lumen (L), with a small amount in the peripheral tubules (arrow) (Lillie's Allochrome). FIG. 3. Day 6. Galactogen is present throughout the gland. The tubules are partially filled (arrows indicate examples of partially filled tubules) (Lillie's Allochrome). FIG. 4. Day 24. Tubules are nearly filled with galactogen (arrows) (Lillie's Allochrome). FIG. 5. Day 30. Tubules are full of galactogen (arrows) (Lillie's Allochrome).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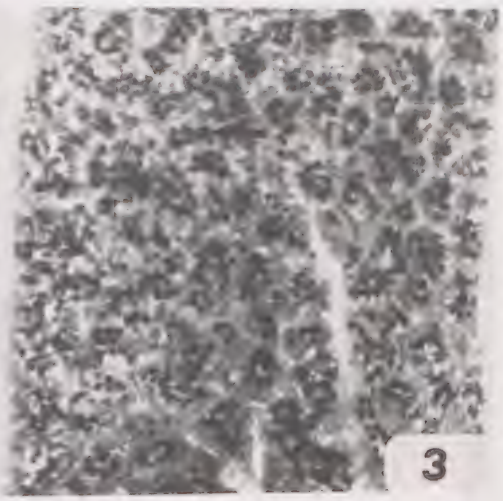
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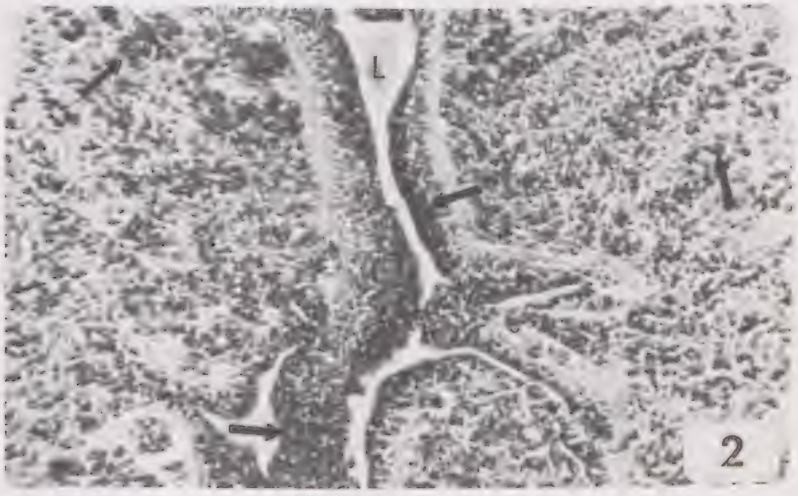
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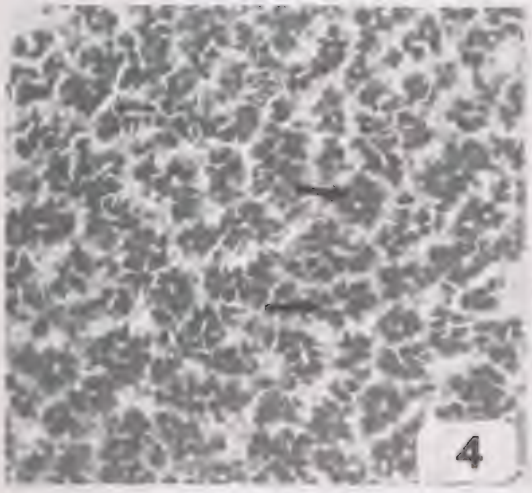
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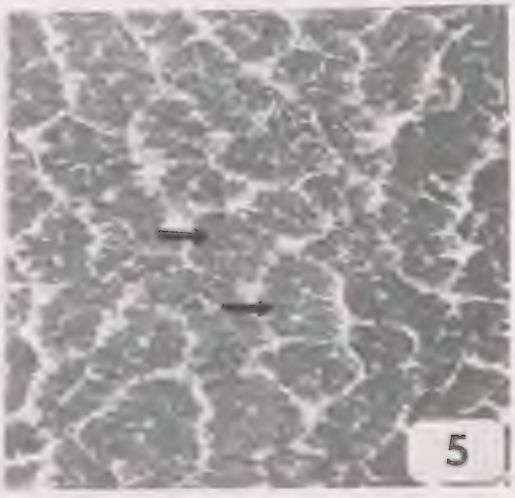
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TABLE 1. Mean weight and carbohydrate content of the albumen gland of *Triodopsis multilineata* during the period from dormancy to 42 days postdormancy.

Time	Total animal	Albumen gland				
	Dry weight (g)[1]	Wet weight (mg)[1]	Dry weight (mg)[1]	Carbohydrate (mg)[1]	% Dry weight[2] $\bar{x} \pm$ S. E.	% Carbohydrate (dry weight)[2] $\bar{x} \pm$ S. E.
Day 0	1.03 (0.84–1.15)	50.1 (36.9–74.9)	17.1 (11.1–26.2)	3.44 (1.59–7.27)	33.6 ± 2.0	20.5 ± 2.0
Day 6	1.23 (1.14–1.38)	59.1 (51.4–73.6)	15.4 (11.3–23.4)	3.34 (1.37–6.62)	25.7 ± 1.4	20.5 ± 2.4
Day 12	1.37 (1.24–1.55)	76.5 (54.0–106.8)	25.4 (16.5–37.2)	11.06 (7.35–19.47)	32.9 ± 0.8	42.7 ± 2.2
Day 18	1.46 (1.34–1.66)	95.6 (71.5–111.4)	34.5 (24.8–41.7)	15.39 (10.25–19.39)	36.2 ± 0.7	45.3 ± 1.6
Day 24	1.41 (1.24–1.53)	80.9 (54.9–120.9)	29.0 (16.5–44.1)	13.52 (7.79–21.17)	35.6 ± 1.1	46.6 ± 0.7
Day 30	1.37 (1.28–1.50)	97.6 (57.8–166.9)	36.5 (19.2–63.1)	15.06 (8.64–25.11)	36.9 ± 0.8	41.9 ± 1.6
Day 36	1.27 (1.17–1.37)	133.7 (62.6–221.5)	50.4 (20.8–86.6)	21.75 (8.99–41.16)	36.6 ± 1.0	42.7 ± 1.2
Day 42	1.24 (1.13–1.37)	115.6 (58.9–194.3)	44.0 (19.2–76.9)	17.82 (9.36–29.75)	37.4 ± 1.0	42.7 ± 1.6

[1]Value for each test day is the mean of 6 samples. Numbers in parenthesis are the range of sample weights for each test day.
[2]Value for each test day is the mean of the percentages of 6 samples per test day.

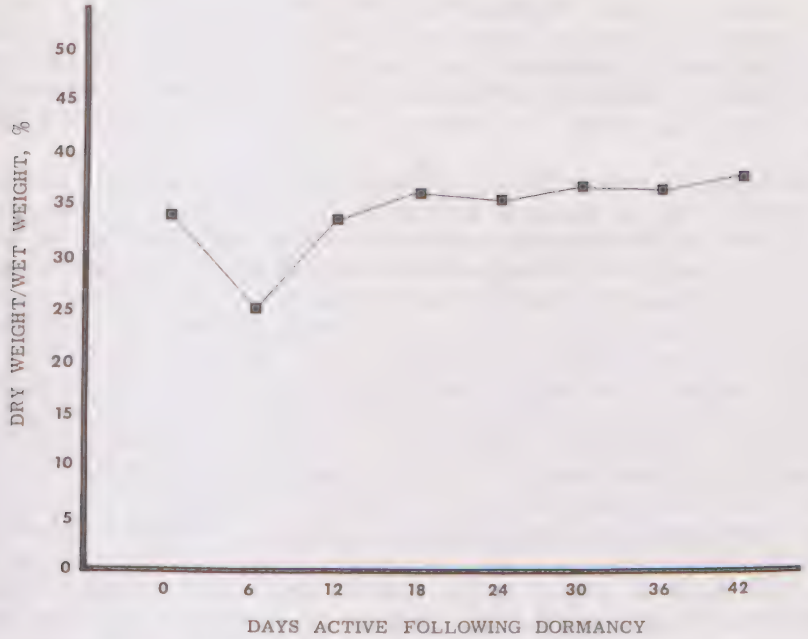

FIG. 6. Ratio of dry weight to wet weight of the albumen gland of *Triodopsis multilineata* during the period from dormancy to 42 days postdormancy.

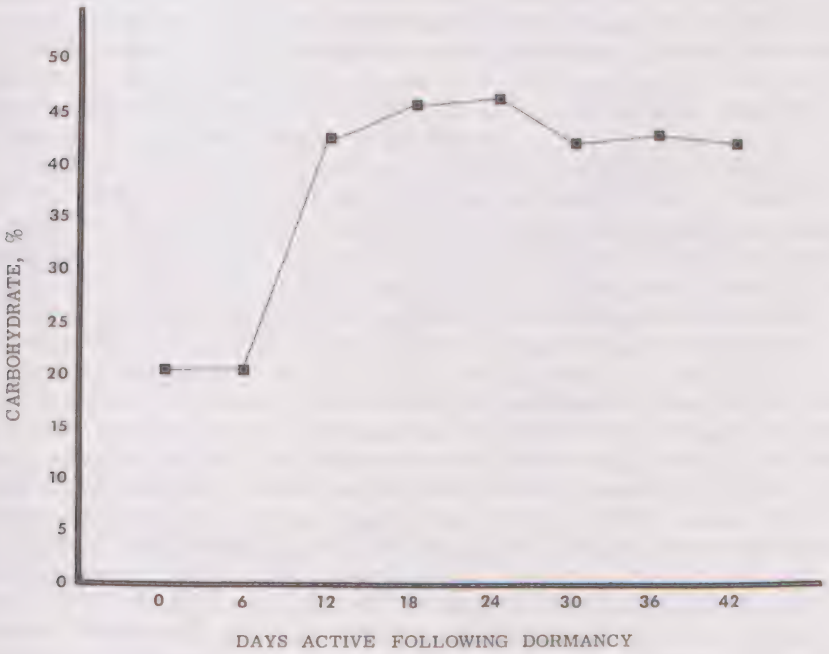

FIG. 7. Ratio of carbohydrate to dry weight in the albumen gland of *Triodopsis multilineata* during the period from dormancy to 42 days postdormancy.

Nieland & Goudsmit, 1969). The deep red PAS-positive granules are unaffected by diastase digestion. Pectinase digestion for 48 hours prior to PAS treatment removes all PAS-positive material. The PAS-positive, diastase-resistant granules are metachromatic with aqueous Toluidine Blue and positive to Best's Carmine, but do not stain with iodine. The above reactions indicate that the granules are galactogen.

The galactogen is present in all animals tested, both dormant and active. In dormant animals (Day 0), different distribution patterns of galactogen can be recognized: (1) the gland may contain almost no galactogen (Fig. 1); (2) galactogen may be present mainly in the regions immediately surrounding the large central duct (Fig. 2), completely filling the cells of this area, with little or none present in cells in the periphery of the gland; or (3) the galactogen may be distributed in fair amounts throughout the gland with a higher concentration in the cells surrounding the lumen. The cells in the periphery of glands from dormant animals are often disrupted and unorganized and the tubular structure found in active glands is often barely recognizable in this area, especially in glands which contain no galactogen. Galactogen present in dormant animals is probably the remaining galactogen from that stored prior to dormancy, as has been shown for *Helix pomatia* and other pulmonates (see Goudsmit, 1972, for a complete review of galactogen in pulmonates) and may vary in amount from animal to animal. In Day 6 animals, galactogen is present in the central area of the gland as in Day 0 animals; however, the peripheral cells are large and are organized into tubules and many cells are 1/2 to 3/4 filled with galactogen (Fig. 3). The galactogen in glands from Day 12 through Day 24 nearly fills all large cells of the gland (Fig. 4). That in glands from Day 30 through Day 42 animals fills all secretory cells of the gland, crowding the nucleus to a position at the outer membrane (Fig. 5).

The dry weight of the albumen gland at Day 0 is 33.6% of the wet weight, drops to 25.7% by Day 6 and rises by Day 12 to 32.9% of the wet weight. The dry weight continues to rise slowly from Day 12 through Day 42 (Fig. 6 and Table 1). Carbohydrate content of Day 0 and Day 6 glands is approximately 20% of the dry weight and is less than all other days. By Day 12, the carbohydrate content has risen to 42.7% of the dry weight. The carbohydrate is somewhat lower each test day after Day 24 but does not fall below 40% of the dry weight (Fig. 7 and Table 1).

The albumen gland appears to become hydrated from Day 0 to Day 6. During this hydration of the gland, there is little change in the carbohydrate level, although histochemical observations indicate that galactogen may be formed by Day 6. Both biochemical and histochemical observations indicate that galactogen is formed at a very rapid rate during the period from Day 6 to Day 12, at which time the tubules become nearly full of galactogen. Subsequent to this initial formation, the cells continue to fill but at a slower rate. The final drop in proportion of galactogen (Day 24 - Day 42) may indicate that the formation of galactogen slows down or stops while other components continue to accumulate, or that the rate of accumulation of other components increases to such an extent that the proportion of galactogen to the dry weight decreases, even though formation of new galactogen may occur.

May (1934) showed that, in *Helix pomatia* albumen glands, the amount of galactogen present nearly reaches its maximum level 6 weeks after cessation of dormancy, but he did not perform any analyses during this 6-week period. In the present study, the galactogen content of the albumen gland of *Triodopsis multilineata* nearly reaches its maximum by Day 12 under laboratory conditions. It remains to be shown that galactogen is present in the eggs of *Triodopsis multilineata*, but it is apparent that galactogen is the main carbohydrate of the albumen gland and that the accumulation of galactogen can occur rapidly after dormancy.

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DYNAMICS OF DDT IN THE TERRESTRIAL SNAIL *OTALA LACTEA* (STYLOMMATOPHORA: HELICIDAE)

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ABSTRACT

Seventy specimens of *Otala lactea* (Müller) were fed 40 μg radiolabelled DDT·gram^{-1} body weight and analyzed by liquid scintillation spectrometry to determine the body distribution and dynamics of the DDT within the snail's tissues.

More than 50% of the pesticide fed to the animals was excreted in the feces after 1-2 days. Residues in the body accumulated mostly in the hepatopancreas. All tissues assayed contained measureable quantities of DDT.

Five patterns of residue distribution/time were apparent. Pattern I, exhibited by the buccal mass, esophagus, crop, stomach and intestine, showed a general decrease in residue concentrations over the 14 day test period. Pattern II, exhibited by the hepatopancreas, kidney, ovotestis, sperm-oviduct, albumen gland and mucous gland showed a general increase in residue concentrations. Pattern III, exhibited by the salivary gland, spermatheca, circumesophageal nerve ring, lung, collar (mantle edge), foot and vagina + dart sack, showed a fairly constant level of residues. Pattern IV, exhibited by the retractor muscles, epidermis and heart, showed a cyclical distribution of residue levels. Pattern V, exhibited by the penis, showed a cyclical distribution of residue levels that was different from Pattern IV.

A double compartment scheme was utilized to explain those trends. Period A, corresponding to the fast compartment, is due to the initial ingestion of insecticide. Periods B and C, corresponding to the slow compartment, are due to the redistribution of residues within the organism.

DDT, once hailed as the panacea to man's insect problems, has within recent years come under increasing attack until, in 1972, its use in the United States was virtually banned. The reasons for this fall to disfavor are numerous and varied and primarily related to the persistence of this toxic chemical in the environment. One of the most serious problems associated with this persistence has been the bioaccumulation and bioconcentration of DDT residues in food webs.

Due to the widespread and often indiscriminate use of insecticides in the past, high levels of these chemicals are often found in the soil ecosystem. Thus, terrestrial gastropods, as members of the soil community, have become increasingly exposed to these compounds. As non-target organisms of many of these chemicals, terrestrial mollusks have been shown to accumulate and concentrate various insecticides without any noticeable deleterious effects at concentrations equal to or higher than concentrations in the soil, their natural habitat. Due to their position in food webs, these animals consequently serve as a concentrated source of these chemicals to their vertebrate and invertebrate predators (Edwards, 1970; Edwards & Thompson, 1973). The organochlorine insecticide 1,1,1-trichloro-2,2-bis(p-chlorophenyl)ethane (DDT) is one of these chemicals.

Residues of this insecticide and its metabolites (degradation products) DDD (1,1-

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TABLE 1. Summary of DDT residues in ppm in terrestrial gastropods recorded in the literature.

DDT residues (ppm) (DDT+DDD+DDE)			Concentration factor	Reference
Organism	Soil	Weight wet or dry		
Slugs				
8.60	–	?	–	Cramp & Conder, 1965
3.44	–	?	–	Cramp & Conder, 1965
10.98	3.28	?	3.3	Cramp & Olney, 1967
6.34	1.02	?	6.2	Cramp & Olney, 1967
38.00	6.00	wet	6.3	Edwards & Thompson, 1973
42.73	–	dry	–	Edwards & Thompson, 1973
19.75	–	dry	–	Edwards & Thompson, 1973
Arion hortensis				
6.20	–	wet	–	Stringer & Pickard, 1965
2.79	–	wet	–	Thompson, 1973
6.53	3.74	wet	1.75	Stringer *et al.*, 1970
Arion spp.				
7.30	2.30	wet	3.2	Davis, 1968; Davis & Harrison, 1966
Milax budapestensis				
35.06	3.74	wet	9.37	Stringer *et al.*, 1970
Deroceras reticulatum				
19.00	2.3	wet	8.3	Davis, 1968
40.10	17.3	wet	2.3	Davis, 1968; Davis & Harrison, 1966
6.50	–	wet	–	Stringer & Pickard, 1965
45.00	–	wet	–	Thompson, 1973
1.75	3.74	wet	0.47	Stringer *et al.*, 1970
p,p' DDT				
18.00	–	wet	–	Davis & French, 1969
36.00	–	wet	–	Davis & French, 1969
60.00	–	wet	–	Davis & French, 1969
Deroceras or *Limax*				
34.47	15.30	dry	2.25	Gish, 1970
45.12	15.30	dry	2.95	Gish, 1970
18.73	3.39	dry	5.53	Gish, 1970
52.70	2.94	dry	17.93	Gish, 1970
24.82	0.51	dry	48.68	Gish, 1970
18.90	–	?	–	Bandy, 1972
Snails (with shell)				
2.21	15.30	dry	0.14	Gish, 1970
3.06	2.94	dry	1.05	Gish, 1970
2.45	2.94	dry	0.83	Gish, 1970

dichloro-2,2-bis(p-chlorophenyl)ethane) and DDE (1,1-dichloro-2,2-bis(p-chlorophenyl)ethylene) were first reported from terrestrial slugs in 1965 by Cramp & Conder who found 3.3 ppm DDE and 5.3 ppm DDD in slugs from an orchard. Slugs from another site contained 0.63 ppm DDE and 2.81 ppm DDD. Stringer & Pickard (1965; cited by Edwards & Thompson, 1973) reported 2.0-10.1 ppm of DDT residues (DDT+DDD+DDE) in slugs from another orchard. Davis & Harrison (1966) reported the following information. Slugs from orchards contained 5.3-23.8 ppm of p,p' (para,para-prime) DDT, 0.4-2.6 ppm of o,p' (ortho,para-prime) DDT, 1.2-9.9 ppm of p,p' DDD and 0.4-3.4 ppm of p,p' DDE. Corresponding residues in the soil were 1.5-13.3 ppm of p,p' DDT, 0.2-1.3 ppm of o,p' DDT, 0.3-0.6 ppm of p,p' DDD and 0.3-2.1 ppm of p,p' DDE. Slugs from cotton fields contained 42.7 and 19.2 ppm of DDT residues (Edwards & Thompson, 1973). Slugs in a strawberry field accumulated DDT and metabolites to more than 70 ppm after spraying with DDT. Prior to the application of DDT, slugs from that field already contained 18 ppm of p,p' DDT. These levels doubled after the 1st treatment and increased to a maximum of 60 ppm after the 2nd treatment. Concentrations of o,p' DDT (about 2.5-10 ppm), DDD (about 2-7 ppm) and DDE (about 1.5-5 ppm) followed a similar pattern at lower levels (Davis & French, 1969).

The information on the bioaccumulation and bioconcentration of DDT residues by terrestrial invertebrates has been reviewed by Thompson (1973). Table 1 summarizes the information available from the literature on DDT residues in terrestrial gastropods.

Little information is available on the fate of DDT within the gastropod body. In an earlier study (Dindal & Wurzinger, 1971) on the helicine land snail *Cepaea*, it was established that most of the DDT in the snail's body was localized in the hepatopancreas and all of the tissues examined contained measurable quantities of the pesticide, which followed several distributional patterns in the course of time. In order to determine whether these same patterns would also occur in other snails, the present study was undertaken using a related land snail, *Otala lactea* (Müller), an edible snail from southern Europe available commercially in the U.S.A. The specific objectives were to determine, after a single feeding of this pesticide: (1) the quantities of DDT that are accumulated and excreted; (2) the tissue concentrations of DDT; (3) the dynamics of DDT in the snail tissues at various intervals after ingestion of the insecticide.

MATERIALS AND METHODS

The snails, *Otala lactea* (Müller), were obtained from Ward's Natural Science Establishment, Inc., and kept in large terraria containing several inches of moist soil covered with leaf litter. The animals were fed lettuce in addition to the litter. Prior to the experimental feeding, they were moved to an empty tank and starved for 2-4 days to flush their digestive tracts of litter material.

A hexane solution of radioactive DDT (purchased from the Radiochemical Centre, Amersham, Buckinghamshire, England) was applied to 15 mm discs of lettuce with a microliter syringe. The animals were fed, once, at a concentration of 40 ug DDT·g^{-1} body weight (with shell) in individual glass culture dishes containing wet filter paper as a source of moisture.

The animals were evaluated in 14 groups of 5 individuals[2] at intervals of 3, 6, 12 and 24 hrs., and 2, 3, 4, 5, 6, 8, 10, 12, 13 and 14 days after ingestion. They were sacrificed by placing them in jars filled with distilled water and then frozen. Placing the animals in the water causes them to extend out of their shells, which facilitates dissection. The animals

[2]Except for the 12 day group in which 1 animal died, leaving only 4 animals to be analyzed.

TABLE 2. Residue concentrations in ppm (wet weight) in *Otala lactea* tissues at various intervals after a single feeding of 40 μg DDT/g body weight

Tissues	Time after ingestion											
	3 hours N=5 mean ± S.E.		6 hours N=5 mean ± S.E.		12 hours N=5 mean ± S.E.		24 hours N=5 mean ± S.E.		2 days N=5 mean ± S.E.		3 days N=5 mean ± S.E.	
Salivary gland	3.05	0.70	3.21	2.21	2.20	1.17	2.63	1.58	1.76	0.73	2.15	1.03
Buccal mass	3.23	1.90	0.96	0.31	0.82	0.19	0.75	0.11	0.72	0.11	0.63	0.25
Esophagus	45.33	8.39	25.18	7.86	8.89	5.14	11.01	5.14	6.09	1.36	13.05	4.52
Crop	127.01	13.93	106.58	16.09	78.12	10.37	114.99	4.13	118.92	31.37	50.01	14.36
Stomach	194.44	85.58	102.72	22.26	64.39	11.53	79.30	5.60	74.57	15.21	36.80	8.78
Intestine	473.31	105.17	573.68	136.91	34.72	22.86	19.66	6.38	75.42	52.64	15.16	9.75
Hepatopancreas (n=10)	58.43	2.76	100.47	12.92	93.88	15.12	178.04	21.79	237.94	55.04	99.79	18.15
Ovotestis	8.88	4.71	10.11	4.12	11.84	5.16	15.68	4.16	12.19	3.12	12.73	5.93
Spermatheca	0.88	0.33	0.60	0.43	0.95	0.66	1.14	0.34	1.07	0.56	0.87	0.74
Albumen gland	0.38	0.18	0.70	0.52	1.00	0.33	0.46	0.12	0.63	0.13	0.81	0.37
Sperm-oviduct	0.15	0.04	0.47	0.30	0.32	0.10	0.26	0.03	0.31	0.09	0.13	0.07
Mucous gland	0.16	0.04	0.43	0.27	0.34	0.14	0.22	0.05	0.47	0.08	1.51	0.72
Vagina + dart sack	0.05	0.02	0.10	0.06	0.16	0.07	0.23	0.13	0.20	0.04	0.27	0.12
Penis + flagellum	0.76	0.55	0.28	0.12	0.16	0.13	0.09	0.06	0.34	0.08	0.53	0.52
Heart	0.81	0.26	0.52	0.20	0.99	0.36	0.71	0.04	0.93	0.08	0.19	0.14
Kidney	0.68	0.08	1.98	0.53	1.85	0.29	1.77	0.23	3.50	1.07	2.63	0.21
Nerve ring	0.15	0.06	0.22	0.06	0.23	0.13	0.11	0.06	0.26	0.11	0.03	0.03
Retractor muscles	0.57	0.13	0.71	0.13	0.73	0.24	0.56	0.24	1.79	1.27	0.52	0.25
Lung (mantle roof)	1.28	0.49	1.42	0.37	1.13	0.13	0.97	0.21	1.09	0.24	1.03	0.45
Epidermis	0.27	0.06	0.39	0.09	0.52	0.16	0.38	0.05	0.78	0.28	0.16	0.09
Collar (n=10)	0.18	0.04	0.33	0.09	0.35	0.05	0.31	0.06	0.47	0.11	0.48	0.24
Foot (n=10)	0.54	0.17	0.54	0.15	1.08	0.34	0.66	0.05	0.86	0.08	0.47	0.23
Digestive tract[1]	190.91	21.35	241.87	51.24	44.93	9.39	58.00	4.24	68.20	19.82	25.73	5.29
Reproductive tract[2]	0.87	0.40	0.83	0.29	1.17	0.48	1.28	0.26	1.59	0.44	1.33	0.57
Body wall[3]	0.38	0.10	0.41	0.07	0.61	0.16	0.44	0.05	0.63	0.09	0.33	0.12
Mucus	1.71	1.50 (n=4)	0.48	0.06	0.66	0.17	0.47	0.09	0.31	0.09	0.42	0.41
Feces (% excreted)[4]	0		0		48.20	2.72	47.30	5.69	44.30	9.85	63.40	5.60

[1] $\sum$μg DDT in salivary gland, buccal mass, esophagus, crop, stomach, intestine/$\sum$weight of these tissues

[2] $\sum$μg DDT in ovotestis, spermatheca, albumen gland, sperm-oviduct, mucous gland, vagina + dart sack and penis + flagellum/$\sum$weight of these tissues

[3] $\sum$μg DDT in epidermis, collar and foot/$\sum$weight of these tissues

[4] (μg DDT in feces/ μg DDT fed to animals) x 100

TABLE 2. (Cont.)

Tissues	Time after ingestion									
	4 days N=5 mean ± S.E.		5 days N=5 mean ± S.E.		6 days N=5 mean ± S.E.		8 days N=5 mean ± S.E.		10 days N=5 mean ± S.E.	
Salivary gland	1.04	0.43	4.81	4.04	1.37	0.36	1.28	0.24	0.58	0.25
Buccal mass	0.40	0.12	0.52	0.11	0.99	0.10	0.23	0.19	2.11	2.04
Esophagus	8.42	4.84	5.82	4.09	35.91	12.23	7.37	3.76	1.23	0.62
Crop	31.91	8.38	11.81	4.82	71.65	15.69	11.65	4.98	11.93	4.09
Stomach	31.27	8.11	30.68	7.82	82.59	22.04	10.75	2.29	14.30	3.51
Intestine	8.01	3.40	68.95	37.44	12.25	1.72	5.86	1.42	8.41	1.63
Hepatopancreas (n=10)	176.96	39.26	278.39	73.60	283.74	18.74	134.12	16.60	104.98	16.76
Ovotestis	19.11	5.05	46.55	16.39	28.07	4.29	19.52	5.64	12.42	3.05
Spermatheca	1.22	0.73	1.88	0.39	0.89	0.24	1.91	1.56	0.50	0.50
Albumen gland	0.82	0.11	3.34	0.74	2.57	0.67	1.08	0.48	1.30	0.31
Sperm-oviduct	0.24	0.02	0.67	0.12	0.56	0.21	0.46	0.24	0.32	0.08
Mucous gland	0.60	0.18	0.78	0.20	1.11	0.50	0.81	0.40	0.54	0.31
Vagina + dart sack	0.19	0.05	0.23	0.05	0.22	0.03	0.35	0.26	0.01	0.01
Penis + flagellum	1.15	1.07	0.66	0.10	0.48	0.09	0.17	0.09	0.03	0.03
Heart	1.04	0.40	1.65	0.42	3.22	1.34	0.71	0.24	0.18	0.11
Kidney	3.03	0.49	4.95	1.48	6.22	1.16	2.89	0.56	2.68	0.55
Nerve ring	0.21	0.09	0.33	0.13	0.28	0.11	0.12	0.07	0.15	0.15
Retractor muscles	0.47	0.08	1.46	0.42	1.36	0.56	0.42	0.13	0.34	0.09
Lung (mantle roof)	0.91	0.35	2.97	0.72	1.34	0.73	0.65	0.17	0.33	0.12
Epidermis	0.37	0.05	0.37	0.14	0.72	0.24	1.10	0.87	0.09	0.06
Collar (n=10)	0.29	0.09	0.40	0.11	0.51	0.11	0.22	0.07	0.05	0.05
Foot (n=10)	0.64	0.16	0.61	0.10	0.57	0.09	0.43	0.08	0.21	0.09
Digestive tract[1]	17.27	3.38	32.97	16.08	31.27	4.08	8.09	1.88	7.42	0.92
Reproductive tract[2]	1.53	0.35	3.36	1.08	2.52	0.75	1.76	0.37	1.09	0.12
Body wall[3]	0.47	0.09	0.48	0.11	0.60	0.13	0.40	0.14	0.18	0.08
Mucus	0.23	0.08	0.15	0.11	0.44	0.36 (n=4)	0.06	0.06 (n=4)	0.09	0.07
Feces (% excreted)[4]	47.20	5.30	60.30	8.60	55.70	2.82	59.10	3.36	69.00	2.10

[1] $\sum$µg DDT in salivary gland, buccal mass, esophagus, crop, stomach, intestine/$\sum$weight of these tissue

[2] $\sum$µg DDT in ovotestis, spermatheca, albumen gland, sperm-oviduct, mucous gland, vagina + dart sack and penis + flagellum/$\sum$weight of these tissues

[3] $\sum$µg DDT in epidermis, collar and foot/$\sum$weight of these tissues

[4] (µg DDT in feces/ µg DDT fed to animals) x 100

TABLE 2. (Cont.)

Tissues	Time after ingestion					
	12 days N=4 mean ± S.E.		13 days N=5 mean ± S.E.		14 days N=5 mean ± S.E.	
Salivary gland	1.88	1.07	0.55	0.19	2.03	1.22
Buccal mass	0.30	0.12	0.31	0.08	0.19	0.06
Esophagus	3.66	1.41	2.36	1.28	1.70	0.50
Crop	7.58	3.00	8.23	2.39	10.05	2.42
Stomach	12.13	3.73	33.83	12.89	9.61	3.22
Intestine	6.55	1.26	19.64	5.89	9.54	5.41
Hepatopancreas (n=10)	217.18	91.35 (n=8)	281.90	53.69	117.86	29.34
Ovotestis	35.48	15.32	45.95	18.23	14.58	4.79
Spermatheca	0.45	0.18	1.24	0.64	0.19	0.19
Albumen gland	2.39	0.61	2.90	1.15	1.50	0.61
Sperm-oviduct	0.44	0.10	0.82	0.36	0.95	0.21
Mucous gland	0.52	0.15	0.72	0.13	0.89	0.34
Vagina + dart sack	0.19	0.05	0.23	0.11	0.08	0.08
Penis + flagellum	0.16	0.06	0.25	0.08	0.24	0.21
Heart	0.93	0.63	0.67	0.16	0.48	0.20
Kidney	3.09	0.81	4.39	0.67	3.51	1.01
Nerve ring	0.17	0.10	0.21	0.06	0.06	0.06
Retractor muscles	0.79	0.44	0.82	0.27	0.57	0.17
Lung (mantle roof)	0.76	0.31	1.37	0.58	0.90	0.55
Epidermis	0.20	0.04	0.24	0.09	0.31	0.13
Collar (n=10)	0.50	0.21 (n=8)	0.29	0.08	0.61	0.16
Foot (n=10)	0.27	0.12 (n=8)	0.67	0.24	0.67	0.25
Digestive tract[1]	11.20	5.91	16.18	3.33	7.70	0.87
Reproductive tract[2]	1.97	0.46	2.69	0.93	1.52	0.33
Body wall[3]	0.33	0.07	0.40	0.10	0.48	0.14
Mucus	0.49	0.46 (n=3)	0.15	0.04	2.01	2.01 (n=4)
Feces (% excreted)[4]	73.00	3.82	69.10	6.14	62.00	9.29

[1] $\sum$µg DDT in salivary gland, buccal mass, esophagus, crop, stomach, intestine/$\sum$weight of these tissues

[2] $\sum$µg DDT in ovotestis, spermatheca, albumen gland, sperm-oviduct, mucous gland, vagina + dart sack and penis + flagellum/$\sum$weight of these tissues

[3] $\sum$µg DDT in epidermis, collar and foot/$\sum$weight of these tissues

[4] (µg DDT in feces/µg DDT fed to animals) x 100

remained frozen at -18°C until they were dissected and analyzed.

Twenty-three tissues (see Table 2) were removed from the treated snails and from 12 control (non-exposed) snails. These tissues were (wet) weighed and prepared for liquid scintillation spectrometry (LSS), which permits a total quantitative assay of the radioactive materials. Each animal was analyzed individually and the DDT content determined for each of its tissues. These individual tissue values were used to obtain the figures in Table 2. In order to determine the pesticide content of the digestive tract, reproductive tract and body wall, the DDT content (µg) of the tissues constituting these glands were divided by the total weight of the tissues. Residues in the left and right lobes of the hepatopancreas were assayed separately and the values obtained were combined for inclusion in Table 2. The various retractor muscles in each animal were assayed as 1 sample. DDT labelled in the p,p' position with ^{36}Chlorine was utilized. This label is of unique analytical significance because the ring structure is not broken during biodegradation; thus all the metabolites produced remained "tagged". With LSS, only DDT and metabolites carrying the isotope label can be counted and no distinction can be made between DDT and its metabolites.

Chlorine-36 is a beta (-) emitter with a relatively high energy (0.714 mev) and a halflife of

4.4×10^5 years. The radioactive DDT had a specific activity of 245 $\mu Ci \cdot g^{-1}$.

Tissue samples were placed in scintillation grade glass vials (22 ml) and put into solution by adding Solulene-^{TM}100 (Packard Instrument Co., Downers Grove, Illinois). The scintillation solution was composed of 5g/l PPO (2,5-diphenyloxazole) as the primary scintillator and 0.3 g/l dimethyl POPOP (1,4-bis(2-(4-methyl)-5-phenyloxozolyl)benzene) as the secondary scintillator dissolved in toluene (Hayes, 1963).

All counting was done on a Packard Tri-Carb Liquid Scintillation Spectrometer Model 3375 containing automatic external standardization equipment. The freezer temperature was maintained at -5°C. The total radioassay count was converted into parts-per-million (ppm) on a wet weight basis. Adjustments were made for counting efficiency and quenching (self-absorption). No untagged insecticide or related compounds within the sample could be counted with LSS.

RESULTS

A total of 294 tissue samples from the non-exposed snails were evaluated by LSS to determine the counts-per-minute (cpm) due to fallout and natural isotopes. Since we were interested only in the maximum levels of activity for each tissue, we used the one tailed t-distribution to calculate the 99% confidence interval (Sokal & Rohlf, 1969). This interval, plus the mean ($\bar{x}$), constitute the background value which was deducted from the scintillation count of each exposed tissue.

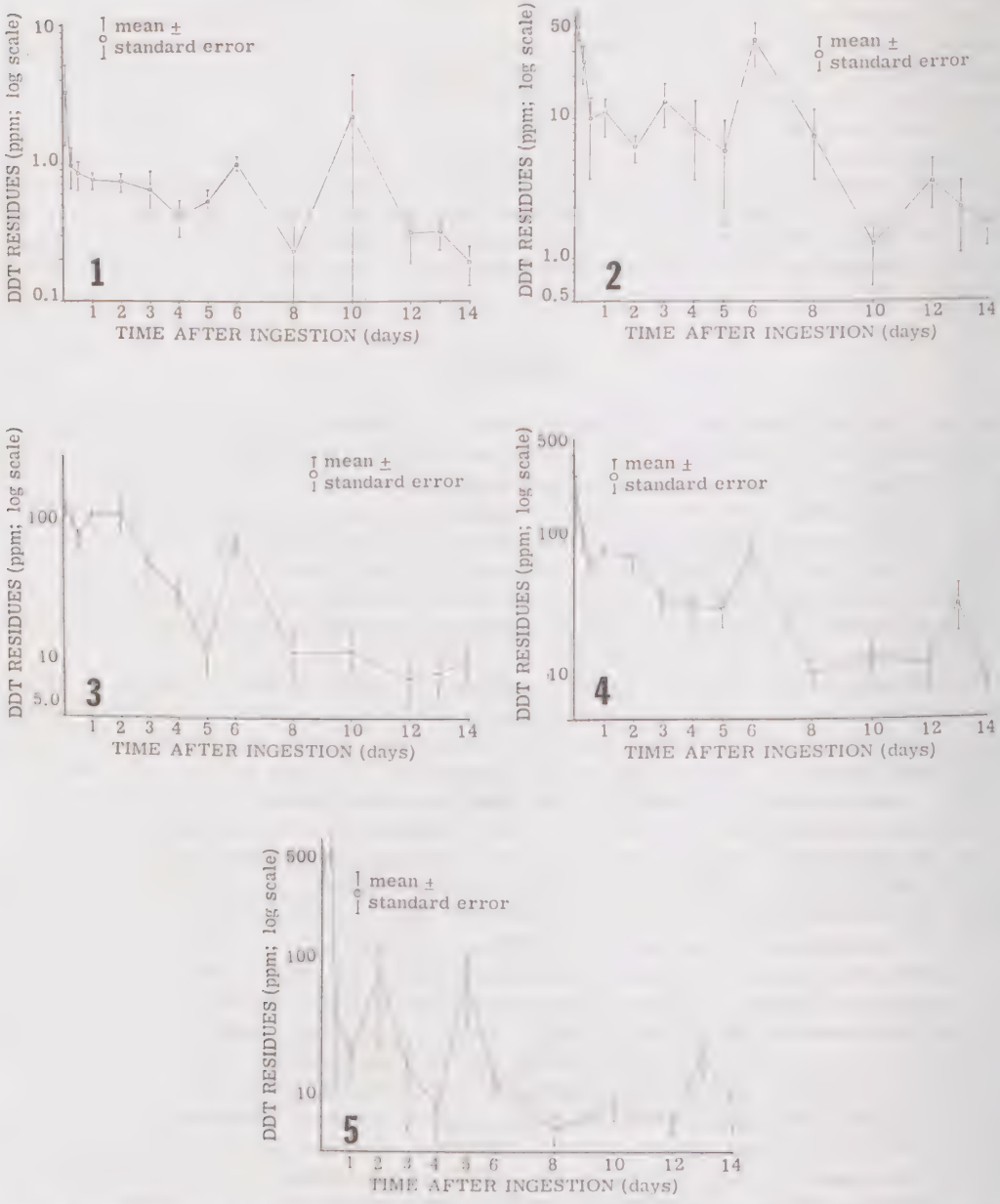
Table 2 and Figs. 1-22 summarize the data obtained from the 14 exposed groups analyzed by LSS. When viewing the graphs, note that the scale on the y-axes is not constant from one graph to another.

The tissues may be arranged into 4 groups according to their decreasing pesticide content. Group I, which containes pesticide levels generally greater than 100 ppm, consists of only 1 tissue, the hepatopancreas. Group II, comprizing tissues that contain between 10 and 100 ppm of DDT residues, consists of the crop, stomach, intestine and ovotestis. Group III, with residue levels between 1 and 10 ppm, consists of the esophagus, kidney, albumen gland, salivary gland and mantle roof (lung). Group IV, comprizing tissues with residue levels generally less than 1 ppm, is the largest and consists of the buccal mass, sperm-oviduct, mucous glands, spermatheca, circumesophageal nerve ring, collar, foot, vagina + dart sack, retractor muscles, epidermis, heart, penis + flagellum and mucus.

A number of different trends are apparent in *Otala*: 5 patterns were distinguished. These consist of rising, falling or basically level residue concentrations on which are superimposed a pattern appearing to exhibit 3 periods: period A, lasting from 0 to 3 days, period B, from 3 to 10 days, and period C, from 10 days onwards.

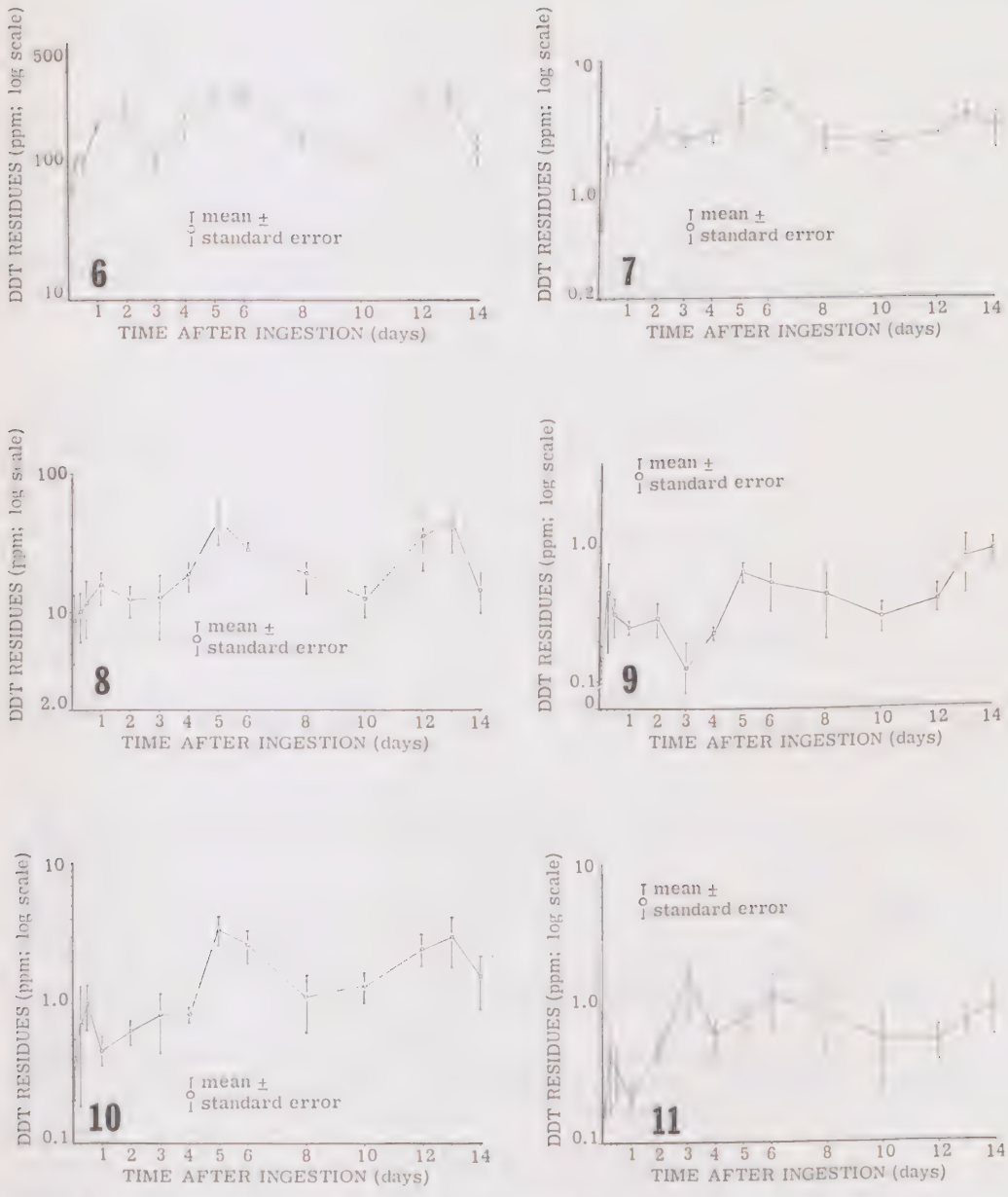
Pattern I, which can be characterized as one of generally decreasing residue concentrations, was exhibited by the following tissues of the digestive tract: buccal mass, esophagus, crop, stomach and intestine. Residue concentrations in these tissues were increasingly higher in the order listed. After 6 hrs., concentrations in the intestine had increased with a concomitant decrease in the residue levels in the other tissues. After 12 hrs., the levels of pesticide were greatly reduced as the animals had excreted part of the intestinal content. The decrease was very rapid in the early exposure periods as the food material containing the pesticide travelled down the gastrointestinal tract. After the gut content had been voided, concentrations stabilized between 1 and 10 ppm, at the level particular for each tissue (Figs. 1-5).

The hepatopancreas, though also part of the digestive system, did not exhibit this pattern (Fig. 6). In this tissue, residue concentrations showed a general increase from a low at 3 hrs. Although the overall trend is an increasing one, there appear



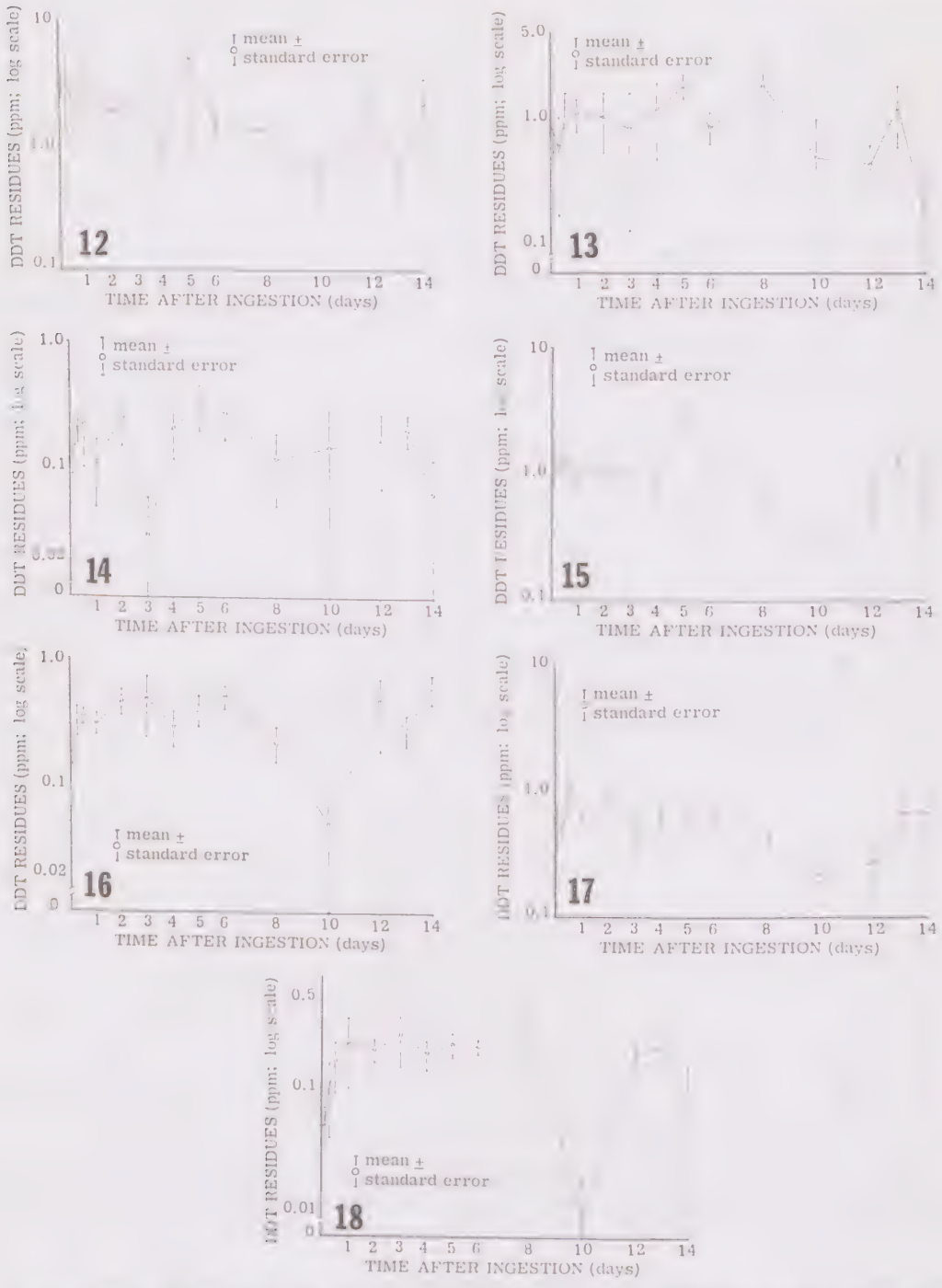
FIGS. 1–5. Pattern I of DDT residue distribution in various tissues of *Otala lactea* during 14 days after a single feeding. FIG. 1. Buccal mass. FIG. 2. Esophagus. FIG. 3. Crop. FIG. 4. Stomach. FIG. 5. Intestine.

in it 3 peaks. Most of the pesticide residues within the snails were concentrated in this gland. Residues in the left lobe, a structure very intimately connected with the intestine which winds through it, were markedly higher than residues in the right lobe (data not shown), which comprizes the bulk of the visceral mass of the snail. This 2nd pattern of residue distribution was also exhibited by the kidney,

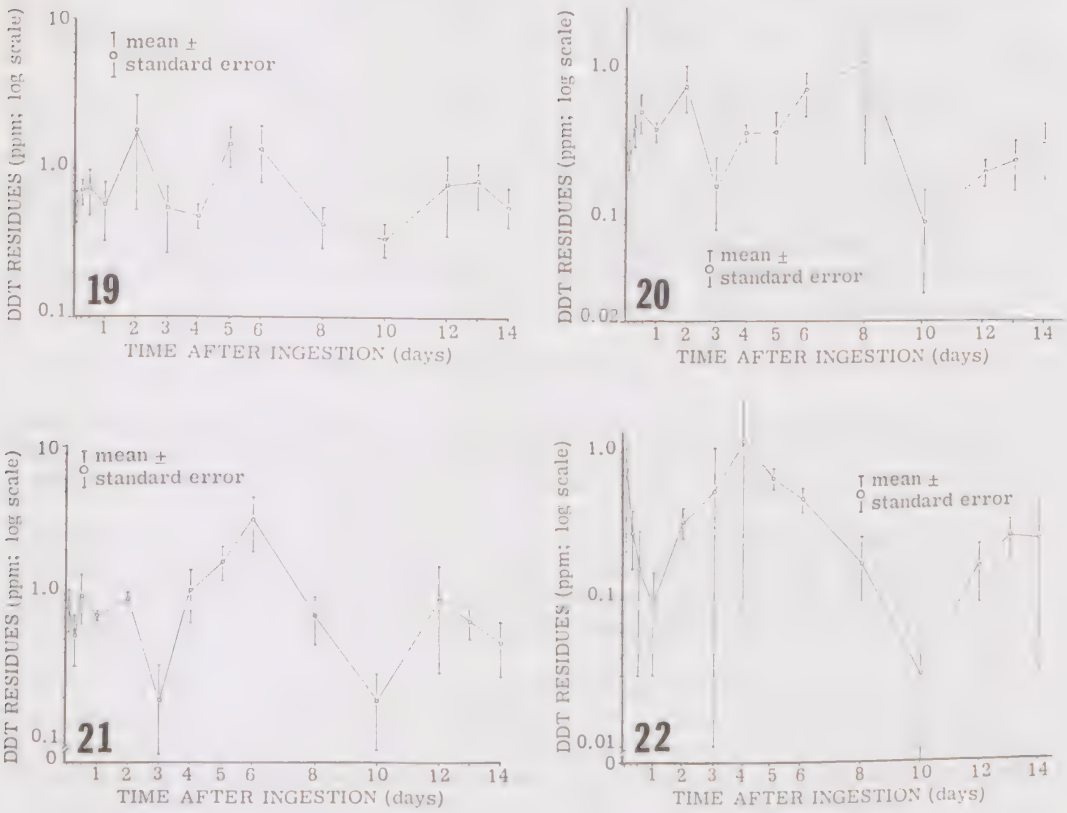


FIGS. 6-11. Pattern II of DDT residue distribution in various tissues of *Otala lactea* during 14 days after a single feeding. FIG. 6. Hepatopancreas. FIG. 7. Kidney. FIG. 8. Ovotestis. FIG. 9. Sperm-oviduct. FIG. 10. Albumen gland. FIG. 11. Mucous gland.

ovotestis, sperm-oviduct, albumen gland and mucous glands (Figs. 6-11). However, residue concentrations in these tissues were considerably lower than those found in the hepatopancreas, which ranged between 100 and 300 ppm. Concentrations in the ovotestis, which is most closely associated with the hepatopancreas, were 6-10 times lower than in the latter. Kidney concentrations were 5-10 times



FIGS. 12-18. Pattern III of DDT residue distribution in various tissues of *Otala lactea* during 14 days after a single feeding. FIG. 12. Salivary gland. FIG. 13. Spermatheca. FIG. 14. Nerve ring. FIG. 15. Lung. FIG. 16. Collar. FIG. 17. Foot. FIG. 18. Vagina and dart sack.



FIGS. 19–21. Pattern IV of DDT residue distribution in various tissues of *Otala lactea* during 14 days after a single feeding. FIG. 19. Retractor muscles. FIG. 20. Mantle. FIG. 21. Heart.

FIG. 22. Pattern V of DDT residue distribution in the penis and flagellum of *Otala lactea* during 14 days after a single feeding.

lower than in the ovotestis, and concentrations in the other 3 tissues were generally 5–10 times lower than in the kidney.

The 3rd pattern of residue distribution was characterized by relatively constant residue levels. It was exhibited by the salivary glands, spermatheca, esophageal nerve ring (brain), mantle roof (lung), collar (mantle edge), foot and vagina + dart sack (Figs. 12–18).

Pattern IV was observed in the retractor muscles, epidermis and heart. These 3 tissues also showed a cyclical distribution of residues, similar to the pattern found in the hepatopancreas. However, the trend is not one of generally increasing residue levels (Figs. 19–21).

Pattern V, exhibited by the penis, showed a cyclical pattern of residues somewhat out of phase with Pattern IV during the early exposure periods. However, after Day 6, these 2 patterns were very similar. This 5th pattern of residue distribution may be a modification of Pattern IV, specific to the penis + flagellum (Fig. 22).

Large quantities of residues were recovered in the feces of the snails. Most of the snails had excreted, after 1–2 days, 50% or more of the pesticide offered to them.

The tissue with the highest residue accumulation was the hepatopancreas. Residues in this tissue often comprized more than 80% of the total residues in the snail body.

For each tissue, residue concentrations after various lapses of time were compared using the Student-Newman-Keuls test. In general, there was no statistically significant difference in the tissue concentrations over the 14 day test period ($\alpha = 0.05$), although differences are apparent visually when residues within each tissue are plotted in respect to time. This lack of statistical significance is probably due to the small sample size and to the high variability within the tissue samples, which may well be a characteristic of terrestrial gastropod tissue and may be related to the open circulatory system of these animals.

DISCUSSION

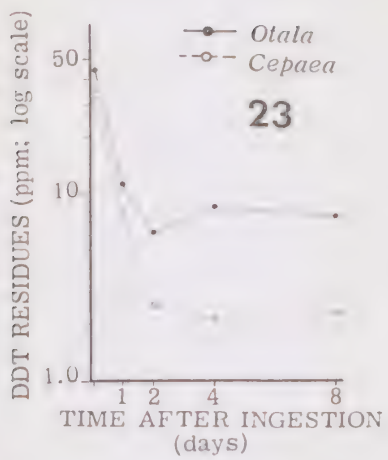
The distributional patterns of DDT residues in *Otala* are, not unexpectedly, very similar to the patterns found in the related genus *Cepaea*. Figs. 23-32 graphically compare the distribution of residues during 8 days in several tissues of these 2 snails.

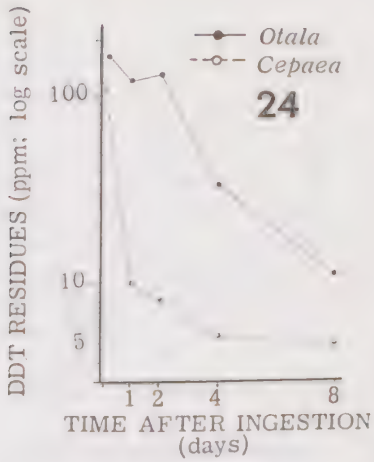
In both species, the animals were never repulsed by the pesticide and, after ingestion, most of the insecticide was excreted in the feces, resulting in lower body concentrations. All tissues contained measureable amounts of residues with the highest levels occurring in the hepatopancreas and to a lesser degree in the ovotestis.

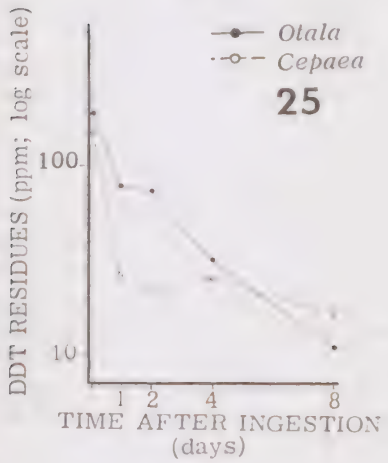
The data obtained for *Otala* suggest tissue storage equilibria. Tissues exhibiting Patterns I and III seem to attain stabilized levels early; although the tissues exhibiting Pattern II show a general increase in residue concentrations, they seem to attain a sort of plateau, especially in the hepatopancreas and kidney. This situation again is similar to that found in *Cepaea*. Chlorinated hydrocarbon residues in mammal and duck tissues have also been reported to exhibit storage equilibria (Hayes, 1965; Dindal, 1970).

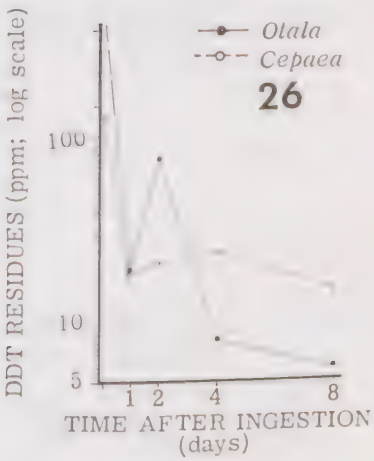
The lipophilic nature of DDT residues in well established (O'Brien, 1967); thus DDT residue levels in snail tissues may be related to their lipid content. This might explain why residues in the hepatopancreas are so high: the digestive cells in this gland contain numerous fat droplets (Sumner, 1965). However, since no information is available as to the actual fat content of gastropod tissues, one can only speculate about possible relationships at this time.

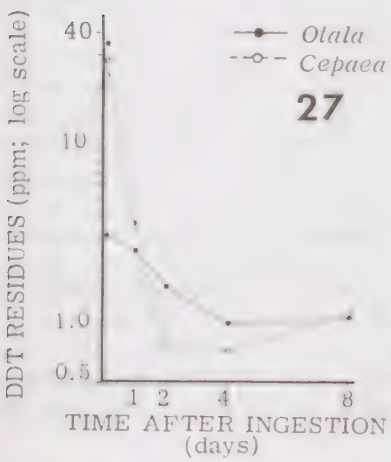
One of the primary defense mechanisms in mollusks is amoebocytic phagocytosis or pinocytosis and subsequent migration of the amoebocytes across certain epithelial layers to the exterior (Tripp, 1970; Sparks, 1972). In this connection, Feng (1965) reported that soluble proteins (e.g., bovine hemoglobin, diptheria antitoxin, *Limulus* serum, rhodamine labeled human gamma globulin and albumin fraction V) were pinocytosed by oyster (*Crassostrea virginica* (Gmelin)) amoebocytes in vivo, and that these amoebocytes migrated across epithelia to the exterior. Amoebocytes in *Biomphalaria* phagocytosed yeast, bacteria and chicken erythrocytes and subsequently migrated across epithelia to the exterior (Tripp, 1963). In *Helix*, thorium dioxide was eliminated on the mantle epithelium (Brown, 1967). This process is perhaps another mode of DDT elimination in *Otala*. Brown found that the maximum concentrations of particle laden amoebocytes in the reproductive tract occurred 4-5 days after introduction of the material into the snail. In *Otala*, there was a peak at 5-6 days in most of the tissues of the reproductive tract, as well as in a number of other tissues. The penis showed a corresponding peak at 4 days. In addition, the epithelium had a peak at 8 days, when the concentrations in the reproductive tract were showing a decline. Thus it is possible that a mode of DDT

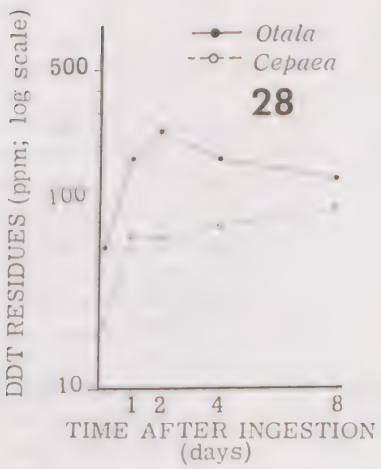




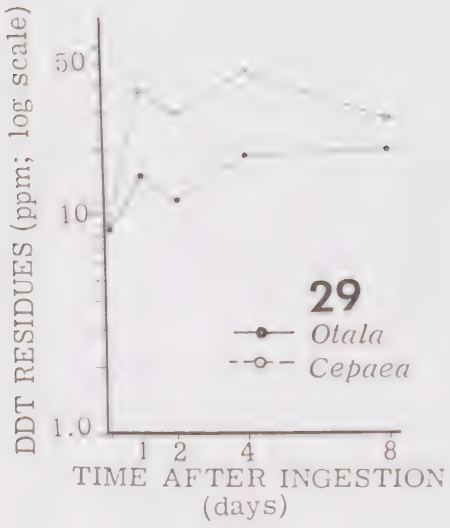


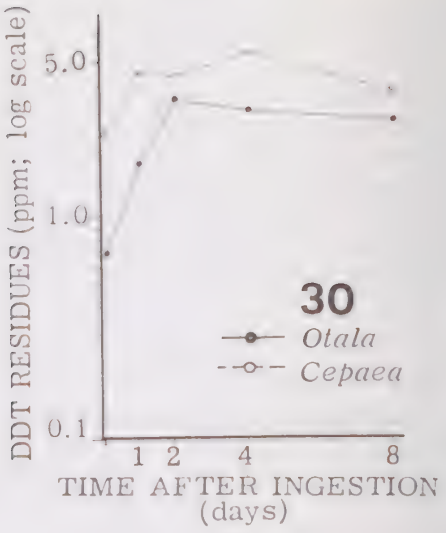


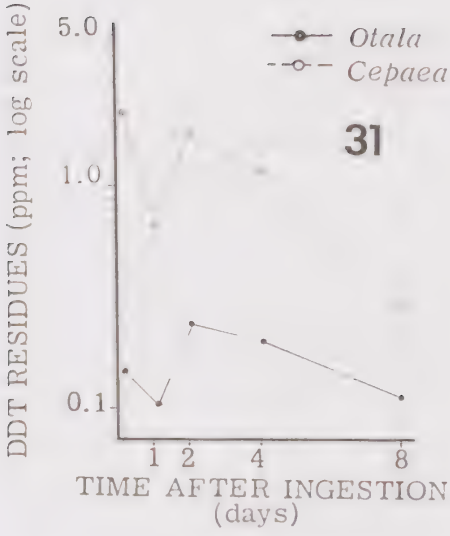


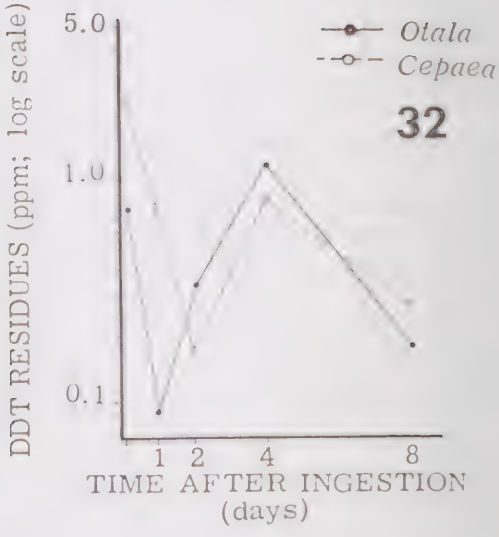


FIGS. 23–28. Comparison of DDT residues in various organs of *Cepaea* and *Otala* during 8 days after a single feeding. FIG. 23. Esophagus. FIG. 24. Crop. FIG. 25. Stomach. FIG. 26. Intestine. FIG. 27. Salivary glands. FIG. 28. Hepatopancreas.









FIGS. 29–32. Comparison of DDT residues in various organs of *Cepaea* and *Otala* during 8 days after a single feeding. FIG. 29. Ovotestis. FIG. 30. Kidney. FIG. 31. Nerve ring. FIG. 32. Penis and flagellum.

elimination in *Otala*, as well as in *Cepaea*, is similar to the process described by Brown (1967), i.e., phagocytosis followed by volatilization or codistillation from the mantle surface.

As indicated above, there appears to be, superimposed on the various residue distribution patterns, a cyclical pattern exhibiting 3 periods. One possible explanation for this might be a scheme similar to the one proposed by Eberhardt, Meeks & Peterle (1970), who modelled a double compartment (fast and slow) scheme to explain the dynamics of DDT in a number of aquatic organisms. The fast compartment is the result of the initial ingestion of the pesticide, and the slow compartment is the result of the redistribution of residues within the organisms. It is possible that the 3 periods found in this study can be explained similarly. Thus period A might very well correspond to the fast compartment and periods B and C to the slow compartment. Perhaps the redistribution of the 2nd phase (period B) is accomplished by amoebocytes and the 3rd phase (period C) by regeneration of exhausted phase 2 amoebocytic activity or perhaps by some as yet unknown mechanism.

Based on the data from *Cepaea* and *Otala*, the following generalizations may be made.

Within helicid snails, there appear to be at least 5 different patterns of residue distribution in the course of time. Pattern I is one of generally decreasing residue levels. It is found in digestive tract tissues and results from the initial exposure to the insecticide. Concentrations decrease rapidly as the food material containing the pesticide passes through the gut and is voided. Residue concentrations in the later time periods are probably due to pesticide that has been absorbed into the lipid fraction of the particular tissues, as well as residues contained in the undigested material excreted from the hepatopancreas, and may well represent pesticide equilibrium levels which are particular to each tissue.

The patterns of residue concentration in the other tissues result from the absorption of residues from the digestive tract and distribution of these residues throughout the body via the circulatory system or some other transport agent. This occurs during period A, when all the tissues receive their initial dose of insecticide. All the tissues contained measureable amounts of residues after 3 hrs.

Pattern II may be characterized by generally increasing residue levels which seem to reach a plateau after a single exposure and appear to stabilize at a value particular for each tissue. Tissues falling into this category are the hepatopancreas and most of the reproductive tract tissues.

The 3rd pattern of residue distribution is characterized by fairly constant residue levels. Once the pesticide reaches these tissues, possibly via the circulatory system, residues are not mobilized to any great extent. Unlike the previous patterns, tissues exhibiting Pattern III are not restricted to any organ system.

The last 2 residue distribution patterns are characterized by a noticeably cyclical distribution of DDT residues. These patterns are found in the retractor muscles, heart, epidermis (Pattern IV) and the penis + flagellum (Pattern V).

Alternatively, when the tissues are grouped according to residue levels found in them, it is found that most of the tissues in the snail body contain rather low levels of pesticide (less than 1 ppm). The greatest amount of pesticide is found in the hepatopancreas, digestive tract tissues and the ovotestis. Several tissues contain intermediate levels of residues. Thus the greatest portion of residues in the snail body is found in the visceral mass. The non-visceral parts of the snail body generally contain relatively low residue levels.

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THE SYSTEMATIC POSITION OF *CYRTONAIAS* (BIVALVIA: UNIONIDAE)

Samuel L. H. Fuller

ABSTRACT

The Central American and Texan freshwater mussel genus *Cyrtonaias* Crosse & Fischer 1894, long of uncertain systematic position, is here determined to be a member of the unionid subfamily Lampsilinae. *Cyrtonaias* is considered to be the most primitive known representative of the Longenae, the most primitive lampsiline tribe. These judgments are based primarily upon the anatomy of Texan specimens of *Unio tampicoensis* Lea 1838, which appears to be identical to *U. berlandierii* Lea 1857, the type species of *Cyrtonaias*. *C. tampicoensis* is homogeneously and delicately papillose along the free mantle margins anteriad from the incurrent mantle aperture and exhibits a marsupium, unique among known Lampsilinae, that occupies the entire outer female demibranch. This species is additionally remarkable for its low degree of sexual dimorphism.

INTRODUCTION

Cyrtonaias was introduced as a section of *Unio* Philipsson by Crosse and Fischer (In: Fischer & Crosse, 1894). The type species of *Cyrtonaias* is *U. berlandierii* Lea 1857, by original designation. In the light of the relevant figures of Lea (1838, 1857) and opinions of Strecker (1931), I agree with the conchologically based judgments of Frierson (1927) and Haas (1969a) that *U. berlandierii* is conspecific with *U. tampicoensis* Lea 1838, which is, also, chronologically first of the many nominal species referred to *Cyrtonaias* by Fischer & Crosse (1894), von Martens (1900), Simpson (1900, 1914), Frierson (1927) and Haas (1969a). Accordingly, I use the combination *C. tampicoensis* (Lea) to typify *Cyrtonaias* in this paper.

Unio tampicoensis and *U. berlandierii* were placed in *Lampsilis* Rafinesque as a subgenus of *Unio* by von Martens (1900). Simpson (1900, 1914) included these species in *Proptera* Rafinesque as a subgenus of *Lampsilis*. Frierson (1927) and Haas (1969a) referred them to *Cyrtonaias* as a subgenus of *Lampsilis*. They were placed in *Lampsilis* without subgeneric designation by Strecker (1931) and Murray & Roy (1968). Haas (1969b) again considered *Cyrtonaias* a subgenus of *Lampsilis*. Finally, other authorities (Modell, 1942, 1964; Morrison, 1967; Heard & Guckert, 1971; Valentine & Stansbery, 1971) have granted *Cyrtonaias* full generic rank. Except for those of Simpson and Frierson, these opinions appear to be uncritical and/or based only upon conchological evidence.

Simpson's (1900, 1914) statement that the marsupium characteristic of his "Group of *Lampsilis umbrosa* [(Lea)]" (in which he included *Unio tampicoensis* and *U. berlandierii*) occupies "the whole outer gills [demibranchs] posteriorly, not projecting much below" is not consistent with Lea's (1860) earlier, accurate observation that the "branchial uterus [marsupium]" of *U. berlandierii* is "filled through the whole length of the outer branchiae [demibranchs]."

Frierson (1927) believed that, were Lea correct, "the group [*Cyrtonaias*] must be placed among the *Elliptio*" (a simplistic response), and he apparently did not consider that Lea (1860) had added, "Branchial opening [incurrent aperture] with papillae on the inner side [inner lobe of the mantle margin], a row of which latter,

diminished in size and wider apart, extends round the basal margin." The latter feature is peculiar to the Unionidae: Lampsilinae (*sensu* Ortmann, 1910) among Nearctic naiades, and, indeed, both of Lea's observations quoted above are consistent with my notes (below) on the anatomy of *C. tampicoensis*.

Often maligned, though sometimes wrongly, Isaac Lea did, in fact and long ago, provide precisely the information needed in order to demonstrate that *Cyrtonaias* belongs, more specifically, to the tribe Lampsilinae: Longenae, recently created by Heard & Guckert (1971). The object of this paper is to support and to amplify this point of view.

MATERIAL

The notes below are based primarily upon 1 male and 1 ovigerous female of *Cyrtonaias tampicoensis* collected 1 August 1972 by Louis E. Sage and myself in the Guadalupe River, about 2 miles southwest of Seguin, Guadalupe County, Texas. (This station is the type locality of *Quadrula* (*Quincuncina*) *guadalupensis* Wurtz 1950 (see Wurtz, 1950).) The material is deposited at the Academy of Natural Sciences of Philadelphia (ANSP). The male specimen is catalogued as ANSP 333535 (the shell) and A4484 (the soft tissues in alcohol); the female as 333535 and A4485.

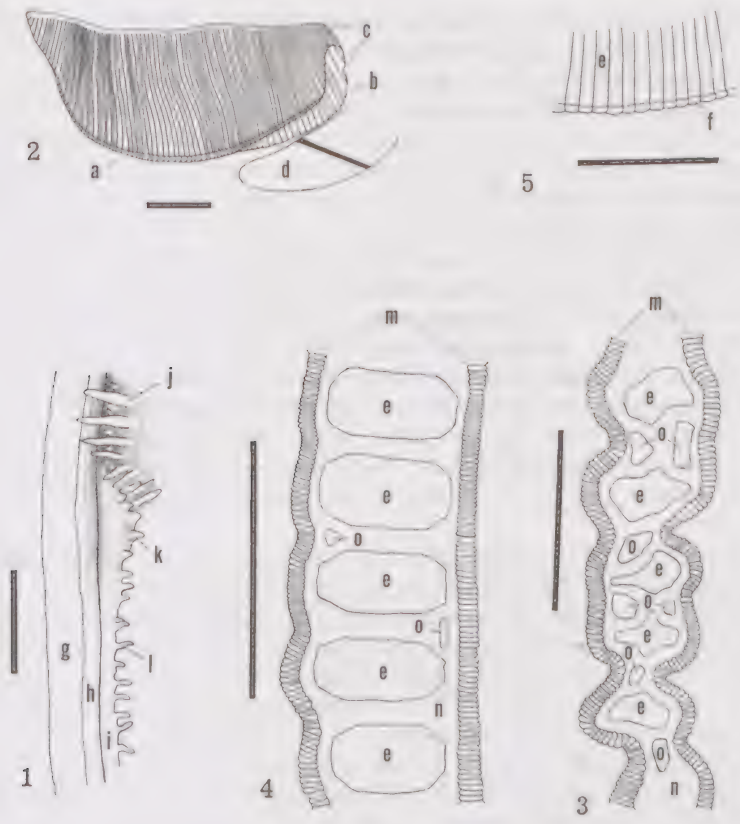
Certain additional observations are included on a series consisting of 10 males, 5 barren females and 1 ovigerous female collected 28 May 1973 by Robert R. Grant, Jr. and myself in the Nueces River at Texas Hwy. 16, about 10.5 miles south of Tilden, McMullen County, Texas. These specimens (ANSP A5266) agree in all essentials with the Guadalupe River material.

All specimens were relaxed with ca. 0.05% sodium nembutal, fixed in ca. 5% formalin and stored in ca. 70% ethanol (tap water was the solvent in these volumetric preparations).

In an attempt to evaluate possible sexual dimorphism in *Friersonia* Ortmann 1912 (the only other genus known in the Lampsilinae: Longenae), large series of shells of *Lampsilis iridella* Pilsbry & Frierson 1908, type species of *Friersonia* by Ortmann's (1912) original designation, and of *L. semirasa* Pilsbry 1909, considered a synonym of *L. iridella* by Haas (1969a), were examined. The series of *L. iridella* are ANSP 93810, the original lot studied by Pilsbry & Frierson (1908); 93810a, the figured holotype, subsequently identified as such by Johnson & Baker (1973); 98555; and 99531 through 99538. ANSP 98555 includes disintegrated material stored in alcohol; this loss is especially unfortunate because, were a male involved, observations on anatomical sexual dimorphism might have been possible as a complement to Ortmann's (1912) diagnosis of *Friersonia*, which is based exclusively on shells and female soft tissues. The series of *L. semirasa* are ANSP 99542, the original lot studied by Pilsbry (1909); 99542a, the lectotype, subsequently selected by Johnson & Baker (1973); and 99539 through 99541. All these materials are from numerous, sometimes poorly localized places in the Gulf drainage of eastern Mexico, chiefly from the Panuco River system (see Pilsbry, 1909).

ANATOMY OF *CYRTONAIAS TAMPICOENSIS*

Differentiation of the free mantle margins is limited to papillation of the inner mantle lobe at and anteriad from the mantle apertures (Fig. 1). There is a single row of short, erect, closely spaced, and rather delicate papillae on the apical surface of this lobe at the anal aperture. There are 2, somewhat intermingled rows at the incurrent aperture (Fig. 1). Those of the outer row closely resemble the anal papillae; the papillae of the inner row are longer, slightly stouter, subtentaculate, and fused basolaterally to the inner surface of the lobe (Fig. 1). The outer row extends anteriad from the incurrent aperture along the apical surface of the inner lobe (Fig. 1) for about 1/2 of the animal's length (cf. Lea, 1860); these



FIGS. 1-5. Aspects of the anatomy of an ovigerous female *Cyrtonaias tampicoensis* (Lea) from the Guadalupe River, about 2 miles southwest of Seguin, Guadalupe County, Texas (ANSP A4485). Scale: the bar equals 5 mm in each figure. Fig. 1. Ventral view of the left post-basal mantle margin at and anteriad from the incurrent mantle aperture. Fig. 2. Lateral view of the right gill and outer oral palpus. Mantle removed along heavy line on palpus. Fig. 3. Transverse section of water tubes in a non-marsupial demibranch (i.e., both demibranchs in the male, as well as the inner ones of the female). Fig. 4. Transverse section of ovigerous water tubes (eggs removed) near the posterior end of an outer, marsupial demibranch. Fig. 5. Lateral view of a portion of the ventral margin of an outer, marsupial demibranch.

Abbreviations used: a = outer, marsupial demibranch; b = inner, non-marsupial demibranch; c = region of fusion of demibranchs to visceral mass; d = outer oral palpus; e = water tube; f = portion of water tube extending distad beyond ventral margins of lamellae of outer, marsupial demibranch; g = outer mantle lobe; h = middle mantle lobe; i = inner mantle lobe; j = papilla of inner row at incurrent mantle aperture; k = papilla of outer row at incurrent (and anal) mantle aperture(s); l = papilla of row along apical surface of inner mantle lobe anteriad from incurrent mantle aperture; m = gill filaments; n = interlamellar tissue; o = vessel paralleling the gill filaments through the interlamellar tissue.

papillae are somewhat longer and more nearly tentaculate anteriad from the aperture (Fig. 1). Immediately anteriad from the incurrent aperture the inner mantle lobe is little wider than it is elsewhere along the margin of the animal (Fig. 1).

The mantle apertures are separated functionally in life by a tangency of the apposing free mantle margins, but there is no mantle suture between them. Anal and supra-anal portions of the excurrent aperture are separated by a suture of the

apposing inner mantle lobes, which is usually about equal to the anal aperture in height. Nine of the 16 Nueces River individuals (or 56.3% of this admittedly small lot) have 1 (4 males) or 2 (4 males, 1 female) secondary suture(s) above the primary suture. This additional occlusion varyingly approaches closure of the supra-anal aperture in a few specimens. The supra-anal aperture lacks papillae and is occluded dorsally for a few mm by postbasad extension of the mantle isthmus. The height of the incurrent aperture is about twice that of the anal, than which the supra-anal is usually a little higher.

The inner demibranch hangs somewhat lower than the outer in the male, and (Fig. 2) posteriorly the outer female demibranch hangs about as low as the inner. The anterior margin of the outer demibranch and about the dorsal 1/2 of the anterior margin of the inner demibranch are fused to the visceral mass (Fig. 2). The dorsal margins of the inner lamellae of the inner demibranchs are either fused to the visceral mass all along the foot or free of the mass for a few mm anteriorly. The dorsal margins of the outer lamellae of the outer demibranchs are free of the mantle for a few mm posteriorly (i.e., the diaphragm is very briefly incomplete), and the gills extend posteriad almost to the mantle margin. Thus the horizontal bar is very short.

Interlamellar septa parallel the gill filaments and are complete, uninterrupted, and imperforate, but the surfaces of the marsupial septa are weakly ribbed transversely, perhaps reflecting phylogenetically recent fusion of adjacent interlamellar connectives (see Fuller, 1971, on the Nearctic unionine genus *Uniomerus* Conrad). Septa of both demibranchs in both sexes occur about every 20 gill filaments (Figs. 3, 4), but in marsupial, outer female demibranchs, septa may be more closely spaced, and in non-marsupial demibranchs of both sexes, the exact spacing may be difficult to determine because of the irregular shapes and sizes of the water tubes. All septa are usually about 10 filaments thick at their bases (Figs. 3, 4), but those of the gravid marsupium are stretched until they become much thinner (Fig. 4). The marsupium occupies the entire outer female demibranch except a few water tubes at each end (Fig. 2). Vessels (Figs. 3, 4) parallel the gill filaments through the interlamellar tissue, which is about equally well developed in each sex; they ordinarily occur at the bases of septa. Vessels are rare and usually minute in the marsupium (Fig. 4), but they are abundant and large in non-marsupial demibranchs (Fig. 3), where, it seems, the septa are formed by fusion of the walls of apposing vessels. Thus the apparent origins of marsupial and non-marsupial septa are quite different. The ventral margins of inner demibranchs are furrowed in both sexes, and those of the outer male demibranchs are sharp, but the marsupial water tubes distend slightly beyond their lamellae (Figs. 2, 5), creating the beaded appearance of the ventral margin of the outer female demibranch.

The egg is subspherical, translucent, apparently minute (see below), and with a subcentral, opaque embryo. The egg mass is compressed from front to rear, narrower below, composed of several layers of eggs, and (see Utterback, 1915: 245, and Fuller, 1971, on the egg mass of *Uniomerus*) reflects the uneven surfaces of apposing marsupial septa. The larval stage, if any, is unknown. I have ovigerous females collected 28 May and 1 August. The nature of the breeding season cannot with certainty be inferred from these data. However, the diameter of the eggs collected 28 May is about 0.16 mm; of those collected 1 August, about 0.17 mm. These data suggest that gravidity commences by at least the late spring in Texas and that development proceeds, slowly, into the fall, perhaps leading to an overwintering larva. This notion contrasts with Morrison's (1967) suggestion that "*Cyrtonaias* . . . may . . . have a short breeding season in the cool winter months" of Mexico.

The outer oral palpi are very slightly larger than the inner. Palpi are large, subfalciform, elongate, and either do not or do barely overlap the inner demibranchs (Fig. 2). The posterior margins of apposing inner and outer palpi are fused together for about the proximal 1/2 of their lengths.

The rectum terminates in a hood, which is slit vertically to form 2 lobes, broader above, whose free margins are crenulate.

Pigment (Fig. 1) consisting of fine dark specks occurs only on the free mantle margins at and for a few mm anteriad from the mantle apertures. The outer mantle lobe and the outer and apical surfaces of the middle lobe are unpigmented. The apposing surfaces of the middle and inner lobes are pigmented. The apical surface of the inner lobe, including its papillae, is unpigmented, and pigment occurs on the inner surface of this lobe among the bases of the papillae of the inner incurrent row. These patterns are poorly developed at the supra-anal aperture and faint to obsolete anteriad from the incurrent one.

SYSTEMATICS OF *CYRTONAIAS*

Classification

Superfamily: The apparent alliance of *Cyrtonaias* to the Lampsilinae: Longenae (see "Subfamily" and "Tribe" below) suggests that its larva, though unknown, will prove to be the glochidium of the Unionacea (see Parodiz & Bonetto, 1963). Moreover, the only alternative is the Mutelacea, whose members' marsupia are restricted to the inner demibranchs (Ibid.), whereas in *Cyrtonaias* the marsupium occurs only in the outer demibranchs.

Family: Assuming that *Cyrtonaias* is unionacean, I place it in the Unionidae (*sensu* Ortmann, 1911, but not as restricted *sensu* Heard & Guckert, 1971) because of the parallel orientation of its interlamellar septa to its gill filaments and because of the location of its marsupium, in the outer, female demibranchs. (The unionacean families Amblemidae and Hyriidae (*sensu* Heard & Guckert), also, satisfy the former criterion, but their marsupia occur, respectively, in all 4 demibranchs and in only the inner ones.) This has been the choice of all authorities save 2: Modell (1942, 1949 [by implication], 1964), who placed *Cyrtonaias* (with all other Lampsilinae) in his Elliptionidae, ostensibly on the basis of beak sculpture (though the only mention of *Cyrtonaias* is in Modell's lists of lampsiline genera); and, apparently, Morrison (1955), who did not mention *Cyrtonaias*, but included the Lampsilinae in his concept of the Amblemidae.

Subfamily: *Cyrtonaias* appears to fall within the Lampsilinae (*sensu* Ortmann, 1910) because it conforms to the one unifying morphological feature of that subfamily (see Ortmann, 1912): distension of the marsupial water tubes ventrad beyond the limits of the lamellae of the outer female demibranchs. This is the concensus of earlier workers, with few exceptions. Morrison (1967) implied that *Cyrtonaias* is a member of his (1955) Amblemidae: Ambleminae. Valentine & Stansbery (1971) uncritically placed *Cyrtonaias* in the Unionidae: Ambleminae. Heard & Guckert (1971) included *Cyrtonaias* in the Unionidae: Popenaiadinae. It appears that Heard & Guckert shared Frierson's (1927) partial appreciation of Lea's (1860) observations on *Unio berlandierii* (see "Introduction" above), which would have led them to the correct assumption that the marsupium of *Cyrtonaias* is restricted to the outer demibranchs, as is characteristic of their concept of the Unionidae. Also, they were influenced by Morrison's (1967) suggestion that "*Cyrtonaias* . . . may . . . have a short breeding season in the cool winter [misquoted by Heard & Guckert as "summer"] months." Now, a bradytictic (i.e., long) breeding season is the one unique

feature of these authors' Popenaiadinae in the context of their concept of the Unionidae, but imputation of bradytixis to *Cyrtonaias* contradicts Morrison's point, even though the winter months are characteristically involved in a long breeding season among Nearctic naiades.

Tribe: On the basis of conchological and anatomical features, Parodiz & Bonetto (1963) usefully employed the tribal concept in their classification of South American naiades; this device may be used to advantage elsewhere in naiad classification. Based on marsupial characters alone, Simpson's (1900) lampsiline subdivisions (Ptychogenae, Eschatigenae, Mesogenae and Heterogenae) are biologically (as well as etymologically) inconsistent with the tribes established by Parodiz & Bonetto, but they are, in effect, of tribal rank. To Simpson's concepts Heard & Guckert (1971) added the Longenae, also based on a marsupial character. The type genus of the Longenae, by monotypy (Ibid.), is the Mexican *Friersonia* Ortmann 1912, whose type species, as noted above (see "Material"), is *Lampsilis iridella* Pilsbry & Frierson 1908, by Ortmann's (1912) original designation. *Friersonia* is remarkable for its marsupium, unique among Lampsilinae and extending all of the height and not quite the length of the outer female demibranch. The marsupium of *Cyrtonaias* is yet more extensive (Fig. 2), and this genus is unquestionably longenous.

Affinities

As discussed above (see "Introduction"), *Cyrtonaias* has been associated, chiefly on a conchological basis, with only *Lampsilis* and *Proptera* among lampsiline genera recognized by Valentine & Stansbery (1971) and by Heard & Guckert (1971). Shells of *C. tampicoensis* do approximate the shape of those of certain species of *Lampsilis* and *Proptera* (see Burch, 1973), but the latter 2 genera have heterogenous marsupia (see Ortmann, 1912). Because *Friersonia* is the only other genus known in the Longenae, only it need be distinguished from *Cyrtonaias* in detail. The differences between these 2 genera are several, including some of great importance, which are evident in the contrast between Ortmann's (1912) notes on *F. iridella* and the anatomy of *C. tampicoensis* given above (plus Lea's (1860) observations on the anatomy of *Unio berlandierii*).

The subcylindrical water tubes of the marsupium of *Friersonia iridella* extend greatly beyond the distal margins of the lamellae of its demibranch and curve posteriad, producing the postbasal margin of the marsupium into a point. The distal margin of the marsupium is rather sharp. The marsupium exhibits dark pigment and is clearly demarked from a short non-marsupial portion of the outer female demibranch at its anterior end. The glochidia are 0.20 mm long and 0.22 mm wide ("of medium size"). The inner lobe of the mantle margin anteriad from the incurrent aperture is crenulate, somewhat broadened, and conspicuously pigmented.

In *Cyrtonaias* the marsupial water tubes extend only slightly beyond the lamellae of the outer female demibranch, thus giving the ventral margin of the marsupium a beaded aspect (Figs. 2, 5). Marsupial water tubes (Fig. 4) are laterally elastic, providing space for a rather broad egg mass. The marsupium (Fig. 2) occupies almost the entire outer female demibranch and is not structurally distinct from the minute non-marsupial region at each end of this demibranch, it is rounded postbasally, and it lacks dark pigment. The eggs are about 0.16 mm in diameter during late May; about 0.17 mm in early August. These data suggest a glochidium smaller than is known for *Friersonia*. Postbasally, the inner lobe of the mantle margin is narrow, conspicuously papillose, and very faintly pigmented (Fig. 1).

In the context of Ortmann's (1912) lampsiline system, the *Friersonia* marsupium is the more advanced in that it occupies less of its demibranch and its water tubes are extended conspicuously posteriad, whereas the *Cyrtonaias* marsupium is the

more advanced by virtue of its laterally elastic water tubes (see Fuller, 1974: 109-110). Similarly, the postbasal mantle margin of *Friersonia* is well developed in terms of pigmentation and breadth (advanced characters), but weakly papillose (primitive character), while *Cyrtonaias* is opposite in these respects. (Finally, the tendency toward closure of the supra-anal mantle aperture in *Cyrtonaias*, though genetically unstable, is an advanced unionid character.) Thus each genus exhibits a different combination of advanced and primitive characters; perhaps each represents a distinct lineage within the Longenae.

The specimens of *Lampsilis iridella* and *L. semirasa* that I have examined (see "Material" above) consist only of unsexed shells, but the lack of 2 distinct, presumably sexual, morphological types in this large quantity of material supports Ortmann's (1912) statement that "Male and female shells [of *Friersonia* are] hardly different." This appears to be true of *Cyrtonaias*, as well. The width/height relationship (an index of obesity, which characteristically differs sexually in the Lampsilinae) of my 10 male Nueces River shells ranges from 55.2% through 68.0%, with an average of 60.3%, while the corresponding figures for the 6 female shells are 58.6% through 67.3%, with an average of 63.8%. Sexual dimorphism of the shell cannot be inferred from these overlapping ranges, and there is no consistent difference in shape between the sexes in these shells. It appears that neither *Friersonia* nor *Cyrtonaias* is in advance of the other in terms of sexual dimorphism of the shell.

There is no other information on sexual dimorphism in *Friersonia*, but it can be emphasized that in *Cyrtonaias tampicoensis* the morphology of the postbasal mantle margin (Fig. 1) in each sex is identical; that in all demibranchs of each sex there is an almost equal development of interlamellar tissue, including equally thick septa (Figs. 3, 4); and that septa, though often set somewhat more closely together in marsupial than in non-marsupial demibranchs, are usually about equally spaced in both types (Figs. 3, 4). Again in the context of Ortmann's (1912) system of the Lampsilinae, the low degree of sexual dimorphism of both hard and soft tissues in *Cyrtonaias* is an extremely primitive feature.

Once distension of the water tubes distad beyond the ventral margins of the marsupial lamellae was achieved, there were evidently 2 major trends in the evolution of lampsiline anatomy (see Ortmann, 1912): restriction of the marsupium posteriad and ventrad in the outer female demibranch and morphological differentiation of the postbasal mantle margin, especially the inner mantle lobe, anteriad from the incurrent aperture. In the former respect, *Cyrtonaias* is undeveloped, and, in the latter, it is weakly developed. Most primitively represented by this genus, the Longenae are probably closer to the original lampsiline stock than is any other extant tribe. Indeed, one or more of the other tribes may bear a deriviative relationship to the Longenae (cf. Heard & Guckert, 1971: 344).

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THE COLONISATION OF HONG KONG'S RAW WATER SUPPLY SYSTEM BY *LIMNOPERNA FORTUNEI* (DUNKER 1857) (BIVALVIA: MYTILACEA) FROM CHINA

Brian Morton

ABSTRACT

The colonisation of parts of Hong Kong's increasingly sophisticated water supply system by the fouling bivalve mollusc *Limnoperna fortunei* (Dunker) has been correlated with a change in the source of supply in 1965 by the Chinese authorities who augment Hong Kong's total water requirements. Such a change involved the utilisation, for the first time, of raw water from the East River, itself a tributary of the Pearl River which is known to be naturally colonised by *Limnoperna*.

The fouling potential of *Limnoperna* is assessed both in terms of Hong Kong and southern China and in terms of the possible introduction of *Limnoperna* to other continental land masses. A warning is given against such an accidental introduction.

INTRODUCTION

With an increasing world population and with affluence, the demand for water is increasing both for drinking, sanitation and industry.

As water supply systems become more sophisticated and a greater efficiency is aimed at, so the potential threat of aquatic fouling organisms becomes more apparent. Of particular importance in this respect are bivalved molluscs.

In Europe, *Dreissena polymorpha* has colonised the rivers, canals, lakes and reservoirs of virtually every north European nation from Russia in the east to Great Britain in the west. Where it occurs in large numbers it may result in the blockage of pipes, channels and aqueducts of domestic and industrial water supply systems (Clarke, 1952) and necessitates the widescale application of chlorine as an antifoulant (Greenshields & Ridley, 1957). In lakes and reservoirs *Dreissena* causes problems of sedimentation. Wiktor (1963), moreover, calculated that the death of *Dreissena* in the Szczecin lagoon, Poland, resulted in the deposition of some 540 tons of shells/km^2/annum. This figure does not take into account the volume of sediments created by the animals as a result of their filtering activities (Stanczykowska, 1968).

In the U.S.A., *Corbicula manilensis* (= *C. fluminalis* (Müller 1774)) was introduced into the Columbia River in the late 19th or early part of the 20th century possibly by Chinese immigrants who, in their native land, utilise *Corbicula* as a source of food. Since its initial discovery in 1938 (Burch, 1944), the species has expanded its range to encompass all of the major North American river basins (Sinclair, 1971a, b). *Corbicula*, like *Dreissena*, is a pest and as well as clogging pipes and condensers also causes problems in gravels which are for ultimate use in the production of concrete.

In India, *Modiolus striatulus* has been recently described as a pest of the Calcutta water supply systems (Krishnamoorthi & Rajagopalan, 1969) where it clogs sand filters and raw water mains. *Modiolus*, unlike *Dreissena* and *Corbicula*, is an estuarine species derived, initially, from the Hooghly River estuary.

In 1968 a further bivalve, *Limnoperna fortunei* (Dunker 1857) (Fig. 1), was found

FIG. 1. External and internal views of the shells of 1 (top) and 2 (bottom) year old specimens of *Limnoperna fortunei*. Length of bottom specimen: 2. 5 cm.

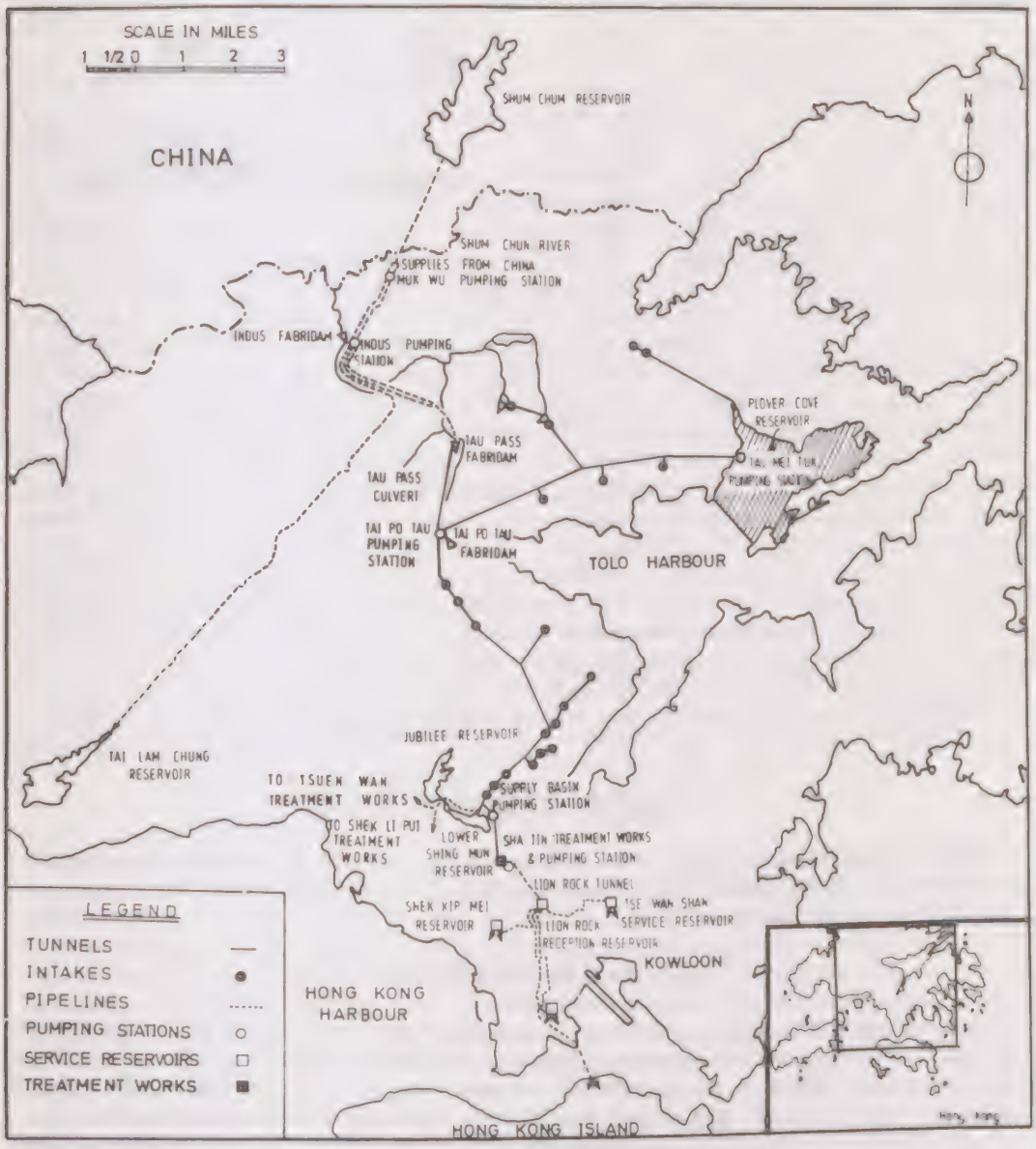

FIG. 2. A map of Plover Cove reservoir and the associated water supply system. The Shum Chun reservoir in China is also figured.

to have colonised parts of Hong Kong's raw water supply system in the New Territories. With the opening in 1967 of Plover Cove (Hong Kong's unique "reservoir in the sea" formed by damming a sea inlet) and the associated supply network of underground tunnels and pipelines, *Limnoperna* has, predictably, extended its range to exploit the great part of this system.

This paper seeks to define a source of infection for *Limnoperna* and to assess the potential threat of *Limnoperna* to Hong Kong's and China's water supply systems.

FIG. 3. Length-frequency histograms constructed from various populations of *Limnoperna fortunei* inhabiting the New Territories water supply system in early and late 1968. Blackened histograms indicate dead populations.

THE INITIAL COLONISATION

In 1966 the 1st specimens of *Limnoperna fortunei* were noted at the inlet main to Shek Lei Pui Filter Station from Kowloon Reception Reservoir (Fig. 2), but the occurrence aroused little interest or comment at the time. In 1967-1968 routine checks of Hong Kong's raw water supply system revealed the presence of *Limnoperna* in large numbers distributed virtually throughout the entire Plover Cove scheme and parts of the associated system in the New Territories. Collections were made throughout 1968 from different sites and the individual specimens constituting the samples so collected were measured along their greatest length. Length-frequency histograms were constructed using this information. Similar length-frequency histograms have been constructed for populations of *Dreissena* in Europe and *Corbicula* from China and have, especially in the former case, been shown to be a useful and reliable index of the time of settlement, period of growth and mortality in these species (Morton, 1969a; 1973a).

For *Limnoperna* it has been shown that in the 1st half of 1968 the population inhabiting the New Territories system comprised a single age class (Fig. 3). Samples collected in the latter 6 months, however, comprised the initial somewhat

larger 1st age class and a 2nd much smaller age class. The 2nd age class had settled during the breeding season of that year, i.e., in 1968. Since there were no further additions to the population in 1968, it would appear that *Limnoperna* reproduces only once a year and therefore that the early unimodal population seen in early 1968 was the result of a 1967 breeding season and probably represented the 1st major, wide scale, colonisation of Hong Kong's raw water supply system. Shek Lei Pui was possibly one of the 1st sites of settlement; the veliger larvae of *Limnoperna* having probably been carried through the supply system in 1965 to raw water termini. By 1966 the animals were large enough to be noticed. However, in 1968, only the 1967 population at Shek Lei Pui was significant, there being no indication of a presumably insignificant 1966 age class. Confirmation of the fact that only 1 major peak of settlement is created by *Limnoperna* each year comes from studies currently in progress in Plover Cove reservoir, some of the results of which are at present available (Morton, 1975). *Limnoperna* possesses a long breeding season and larvae are released in 2 or 3 minor sessions, all of which ultimately coalesce to produce 1 major generation each year. *Limnoperna* and *Dreissena* (Morton, 1969a) do not incubate their eggs. *Corbicula*, on the other hand (Sinclair, 1971a), incubates its young in a ctenidial marsupium. It would thus seem that free-swimming veliger larvae of *Limnoperna fortunei* arrived in Hong Kong in 1965, were carried through the raw water system, settled and were able to produce small breeding colonies, presumably at different sites, but certainly at Shek Lei Pui in 1966. These in turn bred on a much wider scale to produce the 1967 population which settled in sufficient numbers to merit attention. By 1968 a further generation had settled and much of Hong Kong's New Territories raw water supply system was colonised. This included Plover Cove which now comprises a breeding "reservoir" of *Limnoperna* to repeatedly maintain stocks within the tunnel network.

THE SOURCE OF INFECTION

The demand for water in Hong Kong has grown hand in hand with the massive increase in population and the rapidly expanding economy. Supply volumes have risen from 11 million gallons/day in 1924 to 110 million gallons/day in 1965 and to 215 million gallons/day in 1973. As early as 1958, however, it was envisaged that Hong Kong would need further substantial water resources to meet future demands. Thus the Plover Cove scheme was conceived and initiated to produce Southeast Asia's biggest reservoir and to provide a useable capacity of 37,000 million gallons of water by 1967. Arrangements were negotiated with the Chinese authorities, however, to supply extra water to Hong Kong in 1960. This water was pumped to Tai Lam Chung reservoir (Fig. 2) in Hong Kong from the Shum Chun reservoir in China. At the same time local water from the River Indus was also extracted and used the same pipeline. *Limnoperna* was not reported, however, until 1966 and not from the Shum Chun-Tai Lam Chung pipeline until 1968.

In 1965, following a period of severe water shortage and rationing of water in 1963-1964, a second agreement was reached with the Chinese authorities to supply yet more water. In March 1965 the Chinese authorities augmented their supply of water to Hong Kong from the Shum Chun reservoir with water from their recently completed East River scheme. The East River scheme involved the utilisation of the natural water course of the Shih Ma River. It was constructed so that the Shih Ma River, which originally flowed from South to North, was pumped back up hill together with water from the East River to fill the Yen Tien reservoir. From this reservoir the water was pumped along a newly constructed canal to the Shum Chun

TABLE 1. Typical results obtained from an analysis of the raw water supplied to Hong Kong from China. All figures, unless otherwise stated, are in mg/l.

Item tested		Maximum	Minimum	Average
pH		7.0	6.4	6.8
Colour (Hazen)		30	7	12
Turbidity (J. T. U.)		15.2	3.0	6.6
Temperature (°C)		28.0	14.0	22.0
Conductivity at 20°C (Gemmhos)		57	32	45
Ammoniacal N		0.10	NIL	0.03
Albuminoid N		0.11	0.01	0.06
Nitrite N		0.004	NIL	0.001
Nitrate N		0.30	NIL	0.10
Oxygen absorbed value (4 hrs. a 27°C)		1.05	0.28	0.52
Alkalinity ($CaCO_3$)		16	10	14
Total hardness ($CaCO_3$)		17	8	13
Calcium (Ca)		4.8	2.4	3.6
Chlorides (Cl)		8	6	7
Phosphates (PO_4)	total	0.21	0.02	0.08
	ortho	0.10	0.01	0.04
Fluorides (F)		0.13	0.10	0.10
Iron (Fe)		0.11	0.04	0.08
Manganese (Mn)		0.11	0.01	0.03
Silica (SiO_2)		12.9	5.0	7.2
M. P. N. Coliforms/100 ml		564	28	149
M. P. N. E. Coli/100 ml		194	4	35
Plate Count/ml (1 day a 37°C)		282	33	103

reservoir, then via a new pipeline to Hong Kong. China's total commitment to Hong Kong's water supply currently stands at some 18,500 million gallons/annum. The quality of this water is shown in Table 1.

The East River is a tributary of the much larger Pearl River, whose estuary opens up onto Hong Kong's western shores. *Modiolus fortunei* (=*Limnoperna fortunei*) (Miller & McClure, 1931) is a member of the Pearl River fauna and is a pest in that it fouls boats and jetties. *Limnoperna fortunei* has a long breeding season and the larvae settle from January to September under favourable conditions (Morton, 1975). The onset of spawning and the occurrence of planktonic larvae can be correlated with the gradual rise in water temperature following low winter levels. It would seem possible, indeed probable, that free-swimming larvae of *Limnoperna* arrived with the East River water in early 1965. Once settled they would have been virtually unnoticeable and, reaching maturity and spawning in 1966, would have produced a further generation or age class in 1967. These would have in turn produced a 2nd age class in 1968. Their numbers would have been augmented by the continued arrival of larvae each year from China. Such a sequence of events matches almost exactly the known history of *Limnoperna* in Hong Kong.

SUBSEQUENT COLONISATIONS

With the completion of Plover Cove reservoir, a permanent breeding population

of *Limnoperna* has been established in Hong Kong which will infect any system which receives water from it during the mollusc's breeding season. The raising of the reservoir dams in 1973 to increase the useable volume of the reservoir to 51,371 million gallons will facilitate this process by creating new underwater hard shores suitable for colonisation by *Limnoperna*. To date, only the mainland New Territories raw water system is affected, and other raw water supply systems on Lantao Island (fed by the Shek Pik reservoir) and on Hong Kong Island (fed by the Tai Tam and Aberdeen reservoir groups) are unaffected. All of these water systems are fed in turn by local water catchments and thus do not encounter Chinese water from the East River. Should these subsidiary systems need, however, to be put into contact with Chinese water supplies, then there can be little doubt that they too would become infected. Similarly, Hong Kong's latest "reservoir in the sea" - High Island, at present under construction and due to be completed in 1979, with a capacity of some 60,000 million gallons - will also be affected should Plover Cove or Chinese water flow into it.

Moreover, Chinese projects will also be infected should the Pearl River and its tributaries be tapped for further internal supplies. *Limnoperna* has also been reported from Tung-Ting Lake, which connects up with the Yangtsekiang River in Hunan Province (Tchang, Li & Liu, 1955). *Limnoperna fortunei* probably possesses the ability, given water of suitable quality, to colonise whatever water supply systems are constructed, at least in southern China. An accurate picture of the distribution of *Limnoperna* is not available. However, Mizuno & Mori (1970) have reported *Limnoperna lacustris* (=*Limnoperna fortunei*) from the Kwai River, Thailand, where it must also therefore constitute a potential threat to any future water supply schemes.

It is not known if *Limnoperna* is able to survive outside its normal home range which would appear to be tropical and subtropical Southeast Asia; if it can, and we have as yet no reasons for considering otherwise, then *Limnoperna* must be considered a potential threat to other continental land masses and might be transmittable much as *Corbicula manilensis* was earlier this century, possibly also from the Pearl River (Morton, 1973a).

FOULING POTENTIAL

The fouling potential of *Limnoperna fortunei* is high. As noted by Miller & McClure (1931), *Limnoperna* is a fouling species in its natural environment.

In Plover Cove *Limnoperna* occurs in a broad band around the periphery of the reservoir wherever there are rocks. It characteristically colonises crevices and from these foci expands to cover the entire rock surface. Experiments carried out in Plover Cove reservoir with test frameworks have shown that *Limnoperna* preferentially settles at a depth of some 20-30 feet (Morton, 1975) (Fig. 4). It also preferentially settles in differently angled crevices at different depths. In the main, however, shaded horizontal and illuminated vertical surfaces are preferred.

In lakes and reservoirs *Limnoperna* may, especially if the reservoir is new, contribute to the sedimentation of the water mass by virtue of its filter-feeding mode of life. In Europe, *Dreissena polymorpha* is a pest in exactly the same manner (Wiktor, 1963; Stańczykowska, 1968). However, in the initial stages of evolution of a reservoir, such as Plover Cove, *Limnoperna* may be beneficial in assisting in the removal of algae and other suspended material.

In tunnels and pipelines it has been shown that *Limnoperna* initially colonises joints between section lengths and then the general surfaces (Fig. 5A). Significantly the upper horizontal joints of the waterways are colonised first, followed by the

Upper
1
Side
Lower
Upper
2
Side
Lower
Upper
3
Side
Lower
Upper
4
Side
Lower
Upper
5
Side
Lower

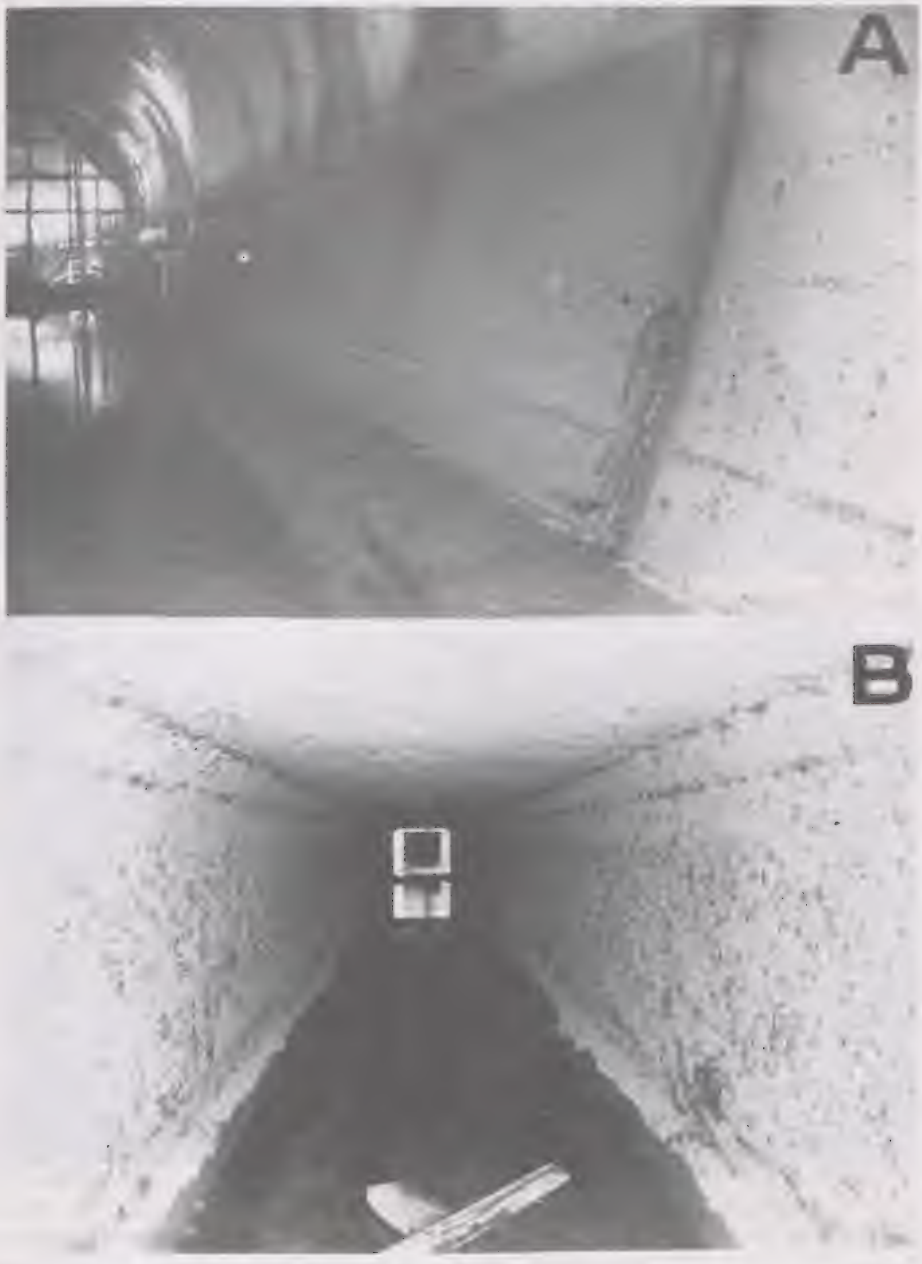

FIG. 5. Light settlement of *Limnoperna fortunei* in the section junctions of (A) a 26 foot (diameter) tunnel from Tai Po Tau pumping station to Plover Cove and (B) a 6 foot wide culvert at Tai Po Tau pumping station.

(opposite page)

FIG. 4. The level of fouling of experimental frameworks hung at 0 [1], 10 [2], 20 [3], 30 [4] and 40 [5] feet in Plover Cove reservoir, after 2 years immersion.

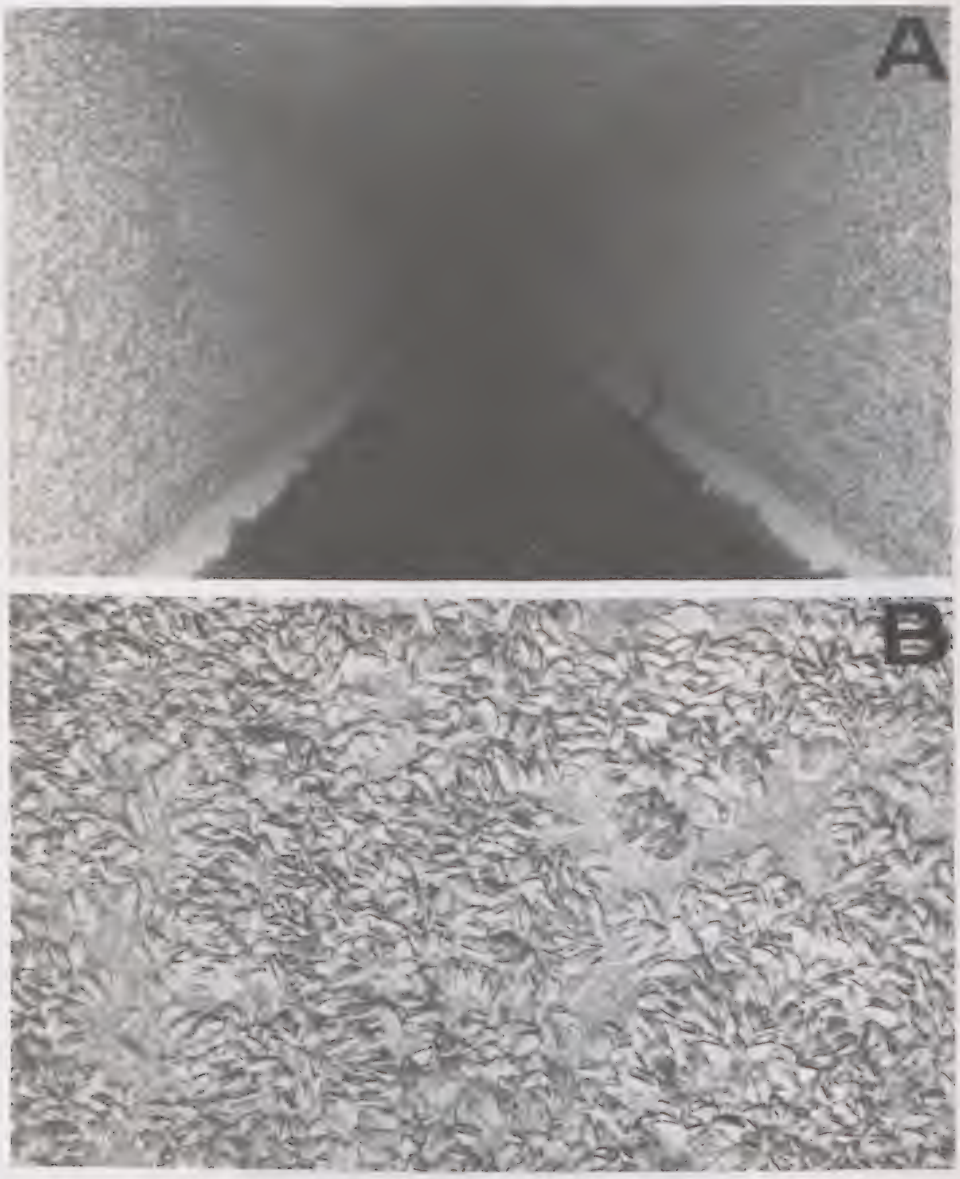

FIG. 6. *Limnoperna fortunei*. A, Dense fouling in a 6 foot wide culvert at Tai Po Tau pumping station. B, A close up of the population inhabiting the culvert at Tai Po Tau pumping station.

lateral vertical junctions. When these are filled, the general surface is colonised (Fig. 5B). Moreover, up to a limit the greater the current through the waterway, the greater the settlement (Fig. 6), though obviously some, as yet undetermined, critical speed must prevail when the larvae cannot settle. Similarly the larvae cannot settle on very smooth surfaces. Noticeably fewer larvae settle on the regions of turbulance within the waterway, e.g., at a bend. Turbulent, as opposed to laminar flow, would seem to be another limiting factor.

There are other factors relevant to the fouling potential of *Limnoperna* which are also of importance. Firstly, *Limnoperna* posesses a thin shell. Such a feature is important, though typical of many other freshwater bivalve phylogenies, e.g., the Unionacea and the Sphaeriacea. It means that in the somewhat acidic and soft waters of Hong Kong and the supplies from China (Table 1) the shell dissolves when the animal dies. Moreover, the laying down of calcium by the mantle in life may also be retarded. The dissolution of the shell after death means, significantly, that as far as the Hong Kong supply system is concerned thick layers of bivalves have not been found to build up with each succeeding generation, as occurs in Europe with *Dreissena polymorpha*, which has a thick shell (Morton, 1969b).

Secondly, studies upon *Limnoperna fortunei* in Plover Cove (Morton, 1975) have shown that this species is comparatively short lived, much like its close relative in estuarine waters, *Musculista senhausia* (Morton, 1974). It has been experimentally shown that *Limnoperna* breeds from January-March to September and that early settlers probably breed within the 1st year of life. After breeding for a 2nd time in the following year, the animals die during their 2nd winter or, at any event, cease growing and are incorporated into the ensuing generation.

Thirdly, like its estuarine relative *Musculista senhausia* (Cheung et al., 1962), *Limnoperna* is prolific; this is evidenced by the speed with which the New Territories water supply system was colonised in numbers which, e.g., in 1968 in the China pipeline, exceeded 11,000 shells/m .

Fourthly, *Limnoperna* possesses a fast rate of growth. It has been shown (Morton, 1975) that *Limnoperna* grows to a length of some 20 mm in its 1st year of life and breeds to produce a 2nd generation. In its 2nd year of life the rate of growth is somewhat slower and the species attains a mean length of some 28 mm, but an occasional length of 32 mm, before dying after having bred for a 2nd time. Only very rarely do specimens survive into a 3rd year.

These 4 factors are all hallmarks of an opportunist species, indicating that *Limnoperna* will settle whenever and wherever it can. As such, it will be difficult to eradicate, the species possessing an inherent adaptability and tenacity suiting it to a variety of life styles.

CONTROL

The problems that *Limnoperna* might cause in water supply systems are divisible into 2 major categories. In reservoirs it may accelerate the rate of sedimentation within the reservoir either by virtue of its filter-feeding activities or by the deposition of shells when the older members of the population die. A reservoir will also act as a ready source of larvae, from the breeding colony it maintains, to repeatedly colonise the supply network.

The monsoonal climate of Hong Kong, with rain falling almost entirely in the summer months, means that the level of the reservoir is lowered each winter. This serves, at present, to limit but not control the growth of *Limnoperna*. In its natural environment, *Limnoperna* probably has few natural predators. In Plover Cove reservoir, however, which was stocked with a variety of fish in an attempt to obtain an ecological balance during the 1st years of its existence, 2 species of fish are known to feed upon bivalve molluscs. These are the Common Carp (*Cyprinus carpio*) and the Mud Carp (*Cyprinus molitorella*). Both *Limnoperna fortunei* and another potential fouling species, *Corbicula fluminea*, are eaten, the latter to a more significant degree.

In raw water mains the presence of *Limnoperna* may result in a reduced flow due to friction loss. This may be the only concern, and a minor one, since it has

been shown that the species does not, at present, produce beds as does *Dreissena* in Europe. If, however, *Limnoperna* should enter the treatment works, as the closely related *Modiolus striatulus* has done in Calcutta (Krishnamoorthi & Rajagopalan, 1969), then the problem could become more acute. Finally, the occurrence of *Limnoperna* throughout the system must be regarded as a potential threat to water quality, especially since the oldest age class must die every year, and if periodic kills of adult populations are made within waterways using a high dosage of chlorine, the ensuing mass mortalities may result in blocked treatment work filters and a deterioration in raw water quality due to the decaying animals.

At present in Hong Kong a 0.5 - 1.0 ppm residual of chlorine is maintained within the distribution side of the treatment plant, which probably helps the filters in preventing entry of the larvae into final water systems. It may ultimately be necessary to dose raw water mains and tunnels with chlorine during the breeding season as is done for *Dreissena* in Great Britain (Greenshields & Ridley, 1957), but to date no studies have been undertaken into the efficacy of chlorine as an antifoulant, since the level of fouling does not, as yet, warrant this. Should *Limnoperna* become troublesome in water systems, a variety of control measures other than chlorine are available and are possibly deserving of consideration.

Most control techniques for *Dreissena polymorpha* have been developed in the U.S.S.R., where this species is particularly troublesome. Control measures currently practised in the U.S.S.R. have been reviewed by Shtegman (1964) and more recently by Mikheev, Dudimkov & Shtern (1969). The latter authors conclude that no single method of control is any longer applicable to *Dreissena* and suggest a wide range of methods suitable for the control of *Dreissena* where it occurs in different water masses. Many of the techniques outlined by these authors may be applicable to *Limnoperna* in Hong Kong and are deserving of acknowledgement should the need for control measures arise.

DISCUSSION

Limnoperna fortunei has colonised part of Hong Kong's increasingly sophisticated water supply system in the New Territories, including Plover Cove, a large "reservoir in the sea" completed in 1967 and enlarged in 1973. Studies upon the population structure of the colonies of *Limnoperna* within the supply system have shown that the initial colonisation probably commenced in 1965 with *Limnoperna* being noted in small numbers in 1966 at one site. In 1967 much larger numbers were reported throughout much of the raw water tunnel network and by 1968 most of the system was colonised and the 1st large scale breeding and settlement had been noted and followed through. In 1974 the problem has not worsened appreciably, and, though *Limnoperna* now coats the internal walls of much of the New Territories raw water supply system, it is not considered a serious pest. Only very recently has friction loss in the main pipeline from China aroused speculation that the pipe is becoming significantly fouled.

The initial colonisation of the new Territories supply system can be attributed to the arrival in Hong Kong of water from the Chinese East River scheme. After 1965 water from China arrived from the Shum Chun reservoir, which was stocked in turn by a newly constructed waterway bringing water from the East River. The East River, a tributary of the much larger Pearl River, is known to be the natural habitat of *Limnoperna fortunei* (Miller & McClure, 1931). Prior to 1965, water arriving from the Shum Chun reservoir was not derived from the East River; significantly *Limnoperna* was not then found in Hong Kong.

Hong Kong has historically relied upon hillside water catchments for its supplies

of fresh water which drain into scattered, usually unconnected small reservoirs. Because Hong Kong is located in the tropics, the supply of water from rainfall is intermittent and largely dependent upon the arrival of the south-west monsoon in summer. With Hong Kong's rapid increase in population since the Second World War, in which the population has risen from some 600,000 to over 4 million, such an irregular and often unpredictable source of supply has been found to be insufficient. Moreover, Hong Kong does not possess natural waterways either big enough or which are unpolluted that could meet such a demand. As a consequence water has been imported from China since 1961. The colonisation of the water supply system by *Limnoperna* reflects the change in water source. Such an event is not new. In Europe, North America and India, water supply systems have respectively been colonised by *Dreissena polymorpha* (Morton, 1969b), *Corbicula manilensis* (Sinclair, 1971b) and *Modiolus striatulus* (Krishnamoorthi & Rajagopalan, 1969) when water has been taken from rivers. Significantly in all cases no screening or purification of the water by chlorination prior to entry into the system has been undertaken, and one must assume that rivers were not biologically surveyed for potential fouling organisms before the waters were tapped. This is also true for Hong Kong and China. One can foresee in Hong Kong on a small scale and China on a much larger scale the steady expansion of range by *Limnoperna* encompassing greater and greater areas as new, interconnected water supply systems are constructed. With the need for greater efficiency in water resources, the problem of *Limnoperna* will compound.

Limnoperna fortunei can be described as an opportunist species combining a fast rate of growth, a long breeding season, high reproductive potential, a free-swimming dispersive larval phase and an ability to quickly colonise all suitable surfaces. *Limnoperna*, as with *Dreissena*, is ideally adapted morphologically (Morton, 1973b) for the colonisation of water pipes containing fast moving bodies of water, but it can also colonise static water masses. It is this ability to colonise a wide range of habitats, as with *Dreissena*, that makes *Limnoperna* so potentially troublesome. In Hong Kong, located as it is on an eroded mountain chain of granitic and volcanic rocks, hardness or calcium levels in the water are low and the shells of *Limnoperna* are dissolved quickly once death occurs. It is not known if such a dissolution would take place in hard waters. If not, then the possibility must exist that beds of *Limnoperna* can be built up.

It has been shown (Morton, 1975) that *Limnoperna* preferentially colonises Plover Cove at a depth of some 20-30 feet. *Dreissena* colonises water bodies at a depth of some 12-20 feet (Morton, 1969a). It is tempting to speculate upon the possible introduction of *Limnoperna* into European or North American water supply systems, each already plagued by 1 species of fouling bivalve. In Europe, the combined effect of *Limnoperna* and *Dreissena* could be catastrophic. Such an introduction is entirely possible. Hanna (1966) has shown how a large number of molluscs have been introduced into the U.S.A., including *Corbicula manilensis*, which was probably introduced from the Pearl River in southern China by Chinese immigrants.

As global water supply systems are forced to become more efficient in supplying the needs of many more people, the problems created by fouling molluscs such as *Dreissena*, *Corbicula*, *Modiolus* and *Limnoperna* are bound to increase.

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BRIEF COMMUNICATIONS

THE CHROMOSOMES OF *VIVIPARUS SUBPURPUREUS* (SAY) (STREPTONEURA: VIVIPARIDAE).[1] — Chromosome numbers have been determined for several hundred molluscan species, including 16 species of the family Viviparidae (Patterson, 1969). However, the morphology of mitotic metaphase chromosomes, i.e., the karyotype, has been presented for less than 1% of these species (Patterson, 1971). This is due, in part, to the difficulties encountered in obtaining adequate chromosome preparations of mitotic chromosomes. Recently several new techniques have been described (Burch, 1968; Patterson, 1971; Stern, 1974) for obtaining better preparations. Karyotype analyses are useful in discerning systematic relationships, although as Burch (1968) noted, most of the few molluscan karyotypes so far determined have dealt with isolated species or at best a few related species.

The species reported on here, *Viviparus subpurpureus* (Say), was collected during the months of October and November, 1973, from Bayou Manchac at its junction with U.S. Highway 61, East Baton Rouge-Ascension Parish Line, Louisiana, U.S.A. The snails occurred in a mud and detritus substrate in nearly stagnant water. As noted by Clench & Fuller (1965), there is pronounced sexual dimorphism in *V. subpurpureus*; females are much larger than males, the right tentacle of the male is swollen to the size of the rostrum to accommodate the penis, and in the female both tentacles are long and pointed (Baker, 1928). Dissection of females collected during the 2 months revealed that 58% (7 of 12) and 96% (27 of 28), respectively, contained embryos in all stages of development. It was advantageous to utilize actively dividing embryonic cells, although all counts and sex determinations were confirmed upon examination of sexually mature adults.

For the examination of embryonic mitotic cells, each of 6 females was injected with 0.2 cc of the spindle fiber inhibitor vinblastine sulfate (Eli Lilly & Co., trade name "Velban") and returned to a dry container. This prevented any loss of the spindle fiber inhibitor from the snails as might have occurred had they been returned to an aquarium. The females were dissected 16 hours later and the embryos removed. Because of their small size (1 mm or less) the embryos were transferred with a pipette. Chromosome squashes from embryonic tissues, as well as from the gonads of adults, were prepared in the manner described by Stern (1974).

The squashes were photographed with a Nikon AFM Microflex 35 mm camera mounted on a Wild compound microscope using Kodak 35 mm High Contrast Copy film. Prints were made on Kodabromide F5 paper.

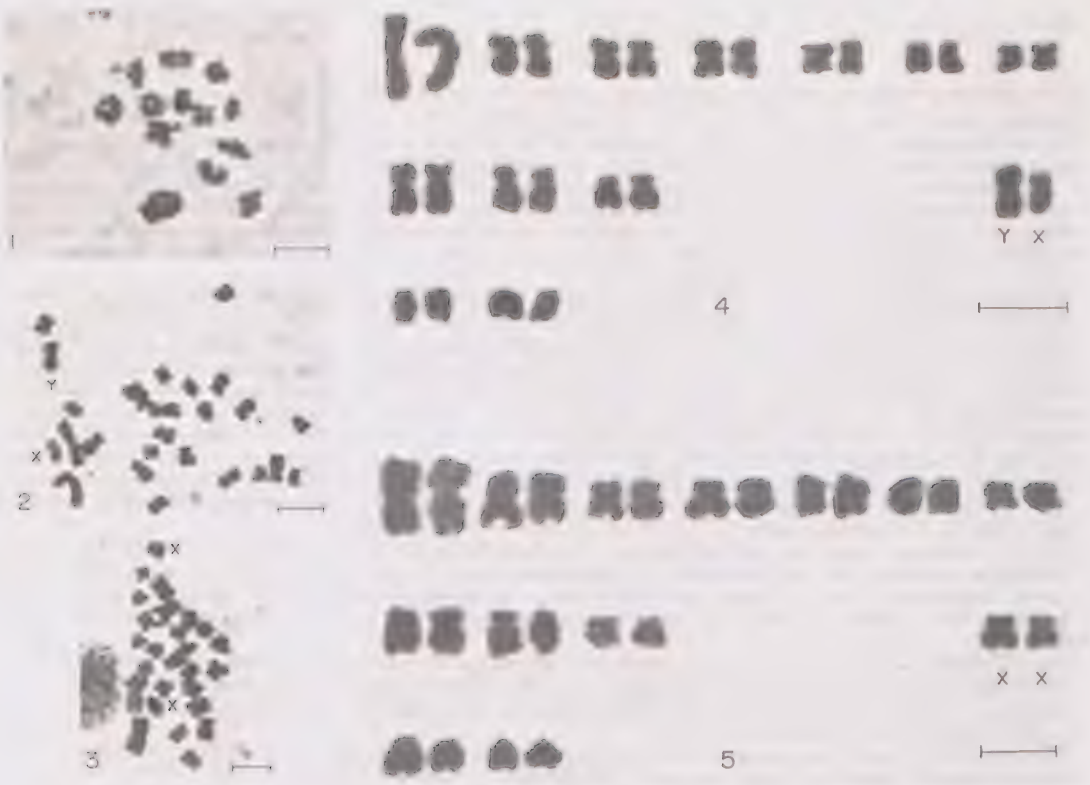
Results. *Viviparus subpurpureus* has a haploid chromosome number of n=13. The diakinesis chromosomes of the male are presented in Fig. 1.

The determination of the somatic karyotype for *Viviparus subpurpureus* is based upon the nomenclature for centrometric position on chromosomes as outlined by Levan, Fredga & Sandberg (1964). Briefly, a chromosome with an arm ratio (long arm/short arm) of between 1.0 and 1.7 is considered a metacentric (medianly constricted) chromosome, while chromosomes with arm ratios of 1.7 to 3.0 are considered submetacentric (submedianly constricted), chromosomes with arm ratios of 3.0 to 7.0 subtelocentric (subterminally constricted) and chromosomes with arm ratios of > 7.0 are considered telocentric chromosomes. The somatic karyotype of *V. subpurpureus* (Figs. 4 and 5) consists of 7 pairs of metacentric chromosomes, 3 pairs of submetacentric chromosomes and 2 pairs of subtelocentric chromosomes. Chromosomal contraction is more nearly complete in the metaphase chromosomes of the female (Figs. 3 and 5) where the largest pair of chromosomes is the 1st pair of metacentrics, which measure 5 micra. The remaining pairs of metacentric chromosomes are intermediate in their lengths. The 1st 2 pairs of submetacentric chromosomes are also intermediate in their lengths. The 3rd submetacentric and both pairs of subtelocentric chromosomes are smaller. Two large chromosomes (Figs. 2 and 4), one medianly constricted (Y) and the other submedianly constricted (X), in the spermatogonial metaphase cells cannot be matched with morphologically similar homologues. In contrast, in the oögonial metaphase spreads, the medianly constricted chromosome is lacking while the submedianly constricted chromosome is paired (Figs. 3 and 5). Therefore, XY is the chromosomal sex-determining arrangement in the male, while it is XX in the female.

Discussion. In an earlier study, Patterson (1965) presented the karyotype for *Tulotoma angulata* (Lea), another viviparid, in which sex chromosomes were identified. The identification of a heteromorphic pair of chromosomes in the male of *Viviparus subpurpureus* substantiates the presence of sex chromosomes in streptoneuran snails. In both instances the sex-determining mechanism is the same, i.e., XX-XY, with the male being the heterogametic sex.

Of the 3 viviparid subfamilies studied, the Viviparinae exhibit the greatest range in haploid chromosome numbers. The haploid chromosome numbers for the genus *Viviparus* range from n=7 for *V. contectus* to n=13 for *V. contectoides* and *V. intertextus*. In contrast, the haploid chromosome numbers of the Bellamyinae, the most primitive viviparid subfamily, range from 8 to 11, while in the Lioplacinae the haploid chromosome range is from 13 to 14 (Patterson, 1969).

Burch (1965) has pointed out that, among the Euthyneura, those species considered more specialized usually also have the greater number of chromosomes. Patterson (1965) applied this hypothesis to the Streptoneura. In an analysis of the gastropods that have been examined cytologically, Patterson (1965) noted that 27% had haploid chromosome numbers less than 18 and even fewer species (12%) had numbers of 14 or less. She concluded that the Viviparidae, where the greatest haploid number is n=14, may be more primitive than had been suggested by Fretter & Graham (1962) and others. The results obtained in this study, where the haploid number for *Viviparus subpurpureus* is n=13, confirms this, at least for the Viviparacea. Such a cytotaxonomic correlation is not, as yet, as clearly evident for other streptoneurans (Patterson, 1969).



FIGS. 1-5. Chromosomes of *Viviparus subpurpureus*. FIG. 1. Diakinesis chromosomes of the male. FIG. 2. Spermatogonial metaphase chromosome spread with X and Y chromosomes labelled. FIG. 3. Oögonial metaphase chromosome spread with both X chromosomes labelled. FIG. 4. Paired homologous chromosomes of the male with X and Y chromosomes indicated. FIG. 5. Paired homologous chromosomes of the female with both X chromosomes indicated. In Figs. 4 and 5, the chromosomes are arranged in decreasing lengths. Scale lines equal 5 micra.

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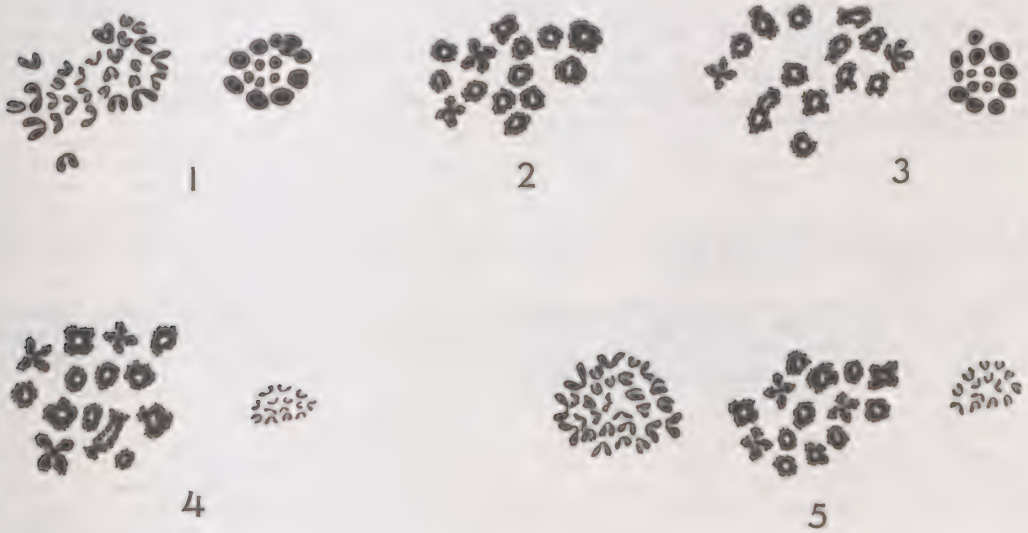
CHROMOSOME NUMBERS OF FIVE SPECIES OF CYCLOPHORIDAE (PROSOBRANCHIA: MESOGASTROPODA) FROM SOUTH INDIA.[1] — A number of studies have been made on the chromosomes of mollusks in recent years, most of which have dealt with chromosome numbers. These studies have been reviewed by Inaba (1961), Burch (1965) and Patterson (1967, 1969). The great majority of the species investigated belong to the class Gastropoda. In the gastropod subclass Prosobranchia (=Streptoneura), to which the 5 cyclophoracean species reported on here belong, chromosome numbers range from n=7 to n=36 (excluding polyploidy) in the 140+ species examined. In the prosobranch order Mesogastropoda, haploid numbers range from n=7 to n=20. But, in spite of these rather wide ranges in numbers, gastropods in general, including the prosobranchs, exhibit a conservatism in regard to change in chromosome number, and within the lower taxa species seldom vary more than ± 2 bivalents (Patterson, 1969).

In the Cyclophoracea, which has Recent species belonging to 5 families, previous information is available for only 2 species (Table 1), each belonging to a different family (Burch, 1967; Rainer, 1967). In both species the haploid chromosome number n=13 was reported.

The chromosomes of only a few species of Indian mollusks have been investigated previously, all in our laboratory. Natarajan (1958a, b, 1959, 1960, 1970) reported on the chromosomes of various opisthobranch and pulmonate gastropods. In the Prosobranchia, Ramamoorthi (1958) studied the chromosomes of 2 species of *Bellamya* (Viviparacea) and Jacob (1959) reported polyploidy occurring in several species of the Thiaridae (Cerithiacea). More recently, Natarajan (1969) investigated the sex chromosomes of *Paludomus* (Cerithiacea). Our present study was undertaken to add to our knowledge of the chromosomes of Indian mollusks, particularly the Cyclophoridae, and also to determine if chromosome numbers could be used for taxonomic discrimination and for showing systematic relationships in this family.

The 5 cyclophorid species we investigated and their localities are listed in Table 1. Gonads of males and females of each species were fixed separately in Newcomer's (1953) fluid; slides were prepared using the aceto-orecein squash technique (LaCour, 1941). All observations were made on freshly fixed material using an Olympus ECE-Tr microscope equipped with a 100X (n.a. 1.25) oil immersion objective and 15X and 20X oculars. Drawings were made with the aid of a camera lucida.

The chromosome numbers n=14, 2n=28 were observed in each of the 5 cyclophorid species (representing 4 genera) we studied (Table 1; Figs. 1-5). We were not able to determine caryotypes or the presence of sex chromosomes. Clearly these cyclophorids of India exhibit the same cytological conservatism that is found in most other mollusks (and chromosome numbers *per se* do not help in their taxonomy). However, the European cyclophorid *Cochlostoma septemspirale* was reported to have only 13 pairs of chromosomes (Rainer, 1967), the same number as the only other cyclophoracean studied, *Pupina* sp. (Pupinidae) of the South Pacific (Burch, 1967).



FIGS. 1-5. Chromosomes (from stages of spermatogenesis) of Indian cyclophorid snails (ca. X1700). FIG. 1. *Cyclophorus jerdoni*; left - mitotic metaphase; right - Metaphase I. FIG. 2. *Pterocyclus bilabiatus*; diakinesis. FIG. 3. *Theobaldius ravidus*; left - diakinesis; right - Metaphase I. FIG. 4. *T. shiplayi*; left - diakinesis; right - Metaphase II. FIG. 5. *Micraulax scabra*; left - mitotic metaphase; center - diakinesis; right - Metaphase II.

TABLE 1. Chromosome numbers in Cyclophoracea.

Species	Haploid number	Source	Reference
Family Cyclophoridae			
Cochlostoma septemspirale (Baden)	13	Europe	Rainer (1967)
Cyclophorus jerdoni (Benson)	14	India*	Present study
Pterocyclus bilabiatus (Sowerby)	14	India	Present study
Theobaldius ravidus (Benson)	14	India	Present study
Theobaldius shiplayi (Pfeiffer)	14	India	Present study
Micraulax scabra (Theobald)	14	India	Present study
Family Pupinidae			
Pupina sp.	13	Solomon Islands	Burch (1967)

*All Indian specimens were collected from Alagarkoil Hills, 13 miles north of Madurai, Tamil Nadu State. *Theobaldius ravidus* was found at an altitude of 1500 ft., *Cyclophorus jerdoni*, *Micraulax scabra* and *Pterocyclus bilabiatus* were found between 2500 and 3500 ft., and *T. shiplayi* was found at 4000 ft. and above.

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SYSTEMATIC STUDIES ON SOME SPECIES OF THE GENUS *HELICIGONA* (PULMONATA: HELICIDAE). — The land snail family Helicidae is well represented in Europe, where there are a great number of Recent and fossil species. Because of the differing opinions of various authors, it might be expected that within this family there will be many discrepancies in taxonomy, particularly in generic divisions and in species assignments, especially since classical systematic characters - the shell and genitalia - may not emphasize any valid generic characteristics. In order to obtain a more accurate assessment of the validity of certain species, we have made use of a biochemical method, starch gel electrophoresis of haemolymph proteins and of muscle and intestine esterases. We have already used this method successfully in separating certain taxonomically troublesome species belonging to the genus *Limax* and *Campylaea* (Grossu & Tesio, 1971, 1972).

Almost all species of the family were at first classified within the single genus *Helix* Linnaeus 1857, a classification based on shell morphology, the one structure common to both living and extinct forms. This morphological character is still being used today for systematic placement of taxa in the Helicidae, and especially for fossils, whose taxonomic assignment must be made exclusively on the form of the shell. Subsequent anatomical studies, based mainly on genitalia, split the former all-inclusive genus *Helix* into many other genera, which were then classified in 8 subfamilies (Zilch, 1960). In such a scheme, it was found that there were a great number of convergences concerning the shell shape, because anatomically very different species belonging to different genera have similar shells. However, recent anatomical studies have also shown the opposite case, where species with very different shells have very similar or identical genitalia, giving rise to much discussion and confusion concerning their identity. In such species, inter- and intrapopulation variation in both shell and anatomy adds to difficulty in identification and classification. For example, based on anatomical studies, such genera as *Cylindrus* Fitzinger 1833, *Chilostoma* Fitzinger 1833 and *Campylaea* Beck 1837 were put into the same subfamily, although their shells are very different. On the other hand, *Campylaea faustina* Rossmässler and *Arianta hessei* Kimakowicz were put into the same genus because they had certain shell characteristics in common (e.g., see Clessin, 1885; Grossu, 1955). The determination of such species are still very difficult, even if we take into account certain indices of variability.

In spite of their well-known genital anatomy, Ehrmann (1932) placed most helicid species within the genus *Helicigona* Risso 1826, including species formerly placed in the subgenera *Drobacia* Brusina 1904, *Chilostoma* and *Campylaea*. Ehrmann left *Arianta* Leach 1831, *Isognomostoma* Fitzinger 1833 and *Cylindrus* as independent genera. However, Zilch & Jaeckel (1962) included *Arianta* in the genus *Helicigona* in their review and supplement of Ehrmann's work. According to Zilch's (1960) classification, which included fossil forms, the species of the subfamily Campylaeinae are distributed into 8 genera of the pre-Quaternary period and 9 Recent genera. *Campylaea*, *Arianta*, *Helicigona*, *Chilostoma*, etc., are treated as independent genera, of which *Chilostoma* is considered to be the most variable and widely distributed genus, and the one having the greatest number of subgenera.

In the present paper we have studied several very similar species of the subfamily Campylaeinae. Our interest in them came from finding in Romania living specimens of *Chilostoma* (*Drobacia*) *maeotica* Wenz, a species morphologically very similar to *C.* (*D.*) *banatica* Partsch (Lupu, 1966). Both species are found as fossils in Europe and have been found alive in Romania only as survivors from the maeotic period. The specimens of *C. maeotica* were determined by shell characters. A question which arose was whether or not *C. maeotica* represents only a subspecies of *C. banatica*, or perhaps even a subspecies of *Arianta arbustorum* (Linnaeus), to which it also has many similarities. A second series of questions regarded the grouping of *C. maeotica* and related species into genera, what criteria are best for showing affinities and making species groupings, and what is the status of the taxa *Arianta* and *Chilostoma* in regard to *Helicigona*.

Materials and methods. The 4 species investigated were collected during the summer of 1971: *Arianta hessei* on the high summits of the Bucegi Mountains (Coştila and Bucura Dumbravă, 2300-2400 m), *Chilostoma maeotica* at Stîna de Vale (Munţii Aspuseni), and *C. banatica* and *A. arbustorum* at Sinaia (Bucegi Mountains). The specimens were collected during the same season and in rather similar climatic conditions. For comparative shell studies of the above species and for those on the genus *Campylaea*, hundreds of specimens were available from many places in Romania. We did not analyse the species of the genera *Isognomostoma* and *Cylindrus*, because these are well defined and do not cause any taxonomic problems. For the biochemical studies we obtained electrophoretic patterns from the haemolymph proteins and the non-specific esterases from muscle and gut extracts. Ten specimens of each species were tested individually. The electrophoresis was performed in 10% starch gel according to the method of Mouray, Moretti & Fine (1961) as modified by the authors (Grossu & Tesio, 1971, 1972). The substrate used to detect esterase activity was alpha naphthyl acetate in Tris-HCl buffer (pH 7.6); esterase activity was visualized with Fast Blue RR. Proteins were stained with a 1% solution of amido black in ethanol-acetic acid-water (4:1:5 parts by volume). Haemocyanin was stained with 0.2% rubeanic acid.

Results and discussion. Shell Morphology. The shells of the 4 species investigated show clear differences in regard to size, color, shape, the presence or absence of carina, and characteristics of the umbilicus. *Arianta arbustorum* has a globose shell with a covered umbilicus, and *A. hessei* has a flattened shell with a widely opened umbilicus (Grossu, 1955). *Chilostoma banatica* has a large, heavily carinated shell, and *C. maeotica* has a smaller, globose shell, very similar to that of *A. arbustorum* (Lupu, 1966). According to shell characteristics, the species appear to be differentiated, although only a trained specialist can easily separate them. However, shells of *A. hessei* and *Campylaea faustina* are difficult to separate, even for the specialist, especially shells which are old or are fossils or subfossils, where the epiphragm is lacking and

shell color cannot be used. In such cases, only an analysis of the spire, the umbilicus and the aperture can be used for differentiation, and even these characters are not really adequate.

Anatomical studies. An analysis of the genitalia of the 4 species led to some interesting observations. A comparative study of the genitalia, organs which are commonly used in gastropod taxonomy, did not show great differences between *Chilostoma banatica* and *C. maeotica* (Lupu, 1966); the basic characters were the same and the size differences were not conclusive. That was also the case between *Arianta arbustorum* and *A. hessei* (Grossu, 1955). More interesting was the fact that the genital anatomy of all 4 species was very similar, although several of the species have been placed previously into different genera. Comparing *C. banatica* and *A. arbustorum* (Fig. 1), there are only minor differences, and one cannot make a clear generic differentiation based only on anatomical criteria.

A comparative analysis of the genitalia belonging to various genera of the subfamily Campylaeinae shows that there are 2 well differentiated types: the 1st, represented by species of the nominal genera *Arianta* Leach 1831, *Chilostoma* Fitzinger 1833 and *Helicigona* Risso 1826, has a simple mucous gland with a single pair of branches; the 2nd type, represented by species of the genus *Campylaea* Beck 1837 (e.g., *C. planospira* Lamarck, *C. trizona* Rossmässler, *C. faustina* Rossmässler and *C. balcanica* Kobelt; these species occur in the Romanian fauna and have been studied by us) has a double mucous gland. According to these anatomical criteria, one may conclude that there are only 2 basic types at the generic level: *Helicigona* (including the nominal genera *Chilostoma* and *Arianta*) with a simple mucous gland (Fig. 1), and *Campylaea* with a double mucous gland.

Electrophoretic studies. No individual variation was found among the 10 specimens of any of the 4 species studied. The electrophoretic patterns of the nonspecific muscle esterases in *Chilostoma banatica* and *C. maeotica* (Fig. 2a, (1) and (2)) differ in the number and the position of the bands. In *C. banatica*, 2 groups of esterases were obtained: one group with 3 bands which show slow or moderate migration, and the other group comprising 3 bands having faster migration. In contrast, in *C. maeotica* all 6 bands had a rapid migration. From this finding we might conclude that the 2 species are distinct and that *C. maeotica* is not a subspecies of *C. banatica*, as one might have concluded from comparing their shells. These species are also different electrophoretically from *Arianta arbustorum* and *A. hessei* (Fig. 2a, (3) and (4)), in spite of their morphological similarities. Additionally, esterases in *A. arbustorum* and *A. hessei* show considerable differences, supporting the distinct morphological differences between the 2 species. The electrophoretic separation of the nonspecific intestine esterases (Fig. 2b) and haemolymph proteins (Fig. 2c) also show similar magnitude of differences between the 4 species, each species being distinct and having a specific pattern of band migrations. In the haemolymph patterns, all 4 species exhibit a common wider and more deeply staining color band having a moderate migration, which demonstrates the presence of haemocyanin.

We believe that the results of the electrophoretic studies are valuable in order to appreciate the validity of the 4 species, since we are assuming that the different patterns obtained by electrophoresis are of sufficient magnitude for species (rather than subspecies) distinction.

Conclusions. From the morphological and electrophoretic studies of *Chilostoma* (*Drobacia*) *banatica* and *C.* (*D.*) *maeotica* on the one hand and *Arianta arbustorum* and *A. hessei* on the other, all very closely related species of the helicid subfamily Campylaeinae, we draw the following conclusions: (1) The shell, currently used for characterizing both fossil and Recent species, is usually adequate to distinguish the 4 species. However, in some instances the shell alone does not provide infallible separation of the species, and since there are known cases of convergence in shell morphology with species of other genera, the shell in the Campylaeinae does not provide a reliable basis for generic distinction, nor is it adequate for showing phylogenetic relationships. (2) In all 4 species the genitalia are so similar that they are not adequate for use in species separation. Therefore, if we weight this character heavily, we can place the 4 species in the same genus, to which the name *Helicigona* Risso 1826 should be applied because of its nomenclatural priority. This genus can be characterized by the presence of a mucous gland composed of a single paired branch, and it includes as synonyms the nominal genera *Arianta* and *Chilostoma*. (3) *Campylaea* Beck 1837 should include all species which have a mucous gland composed of a double pair of branches. Other European species may also have to be assigned to one or the other of these 2 genera, i.e., *Helicigona* or *Campylaea*. Our anatomical studies further indicate that subdividing either genus into subgenera does not seem to be justified. (4) We believe that our electrophoretic analyses indicate that *H. maeotica*, known before only from fossils, is a distinct species and not a subspecies of *C.* (=*H.*) *banatica*, as previously thought. Further, the electrophoretic analyses support anatomical evidence that *H. hessei* is distinct from *Campylaea faustina* (even though both species have very similar shells). Anatomically, *H. hessei* seems to be closely related to *H. arbustorum*.

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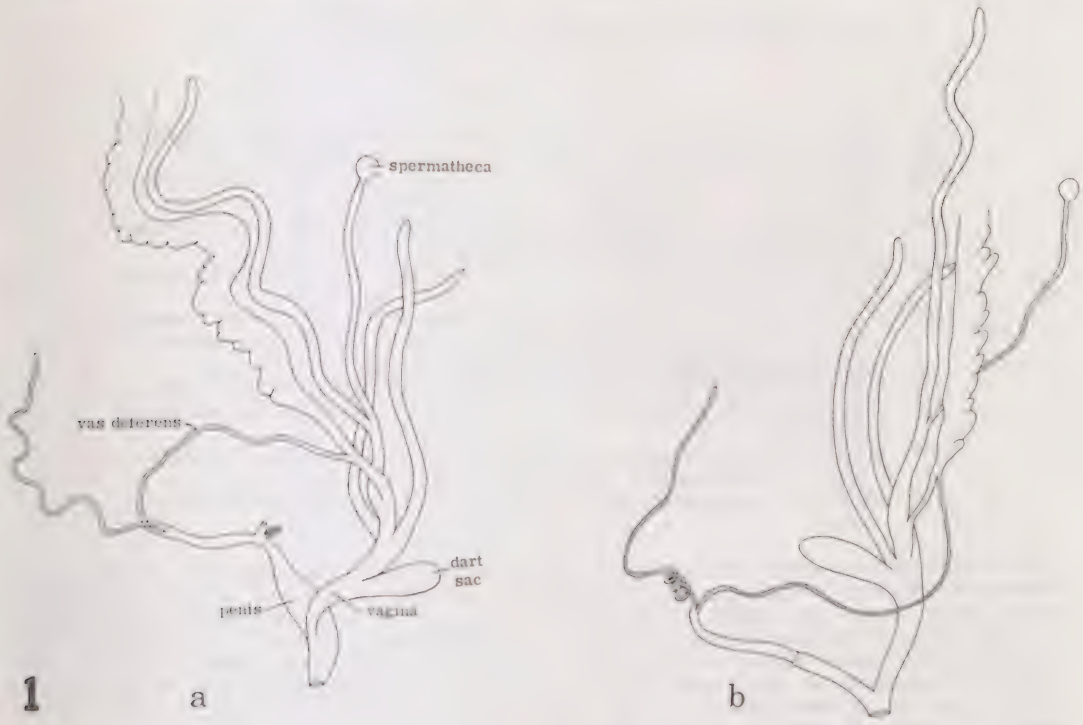

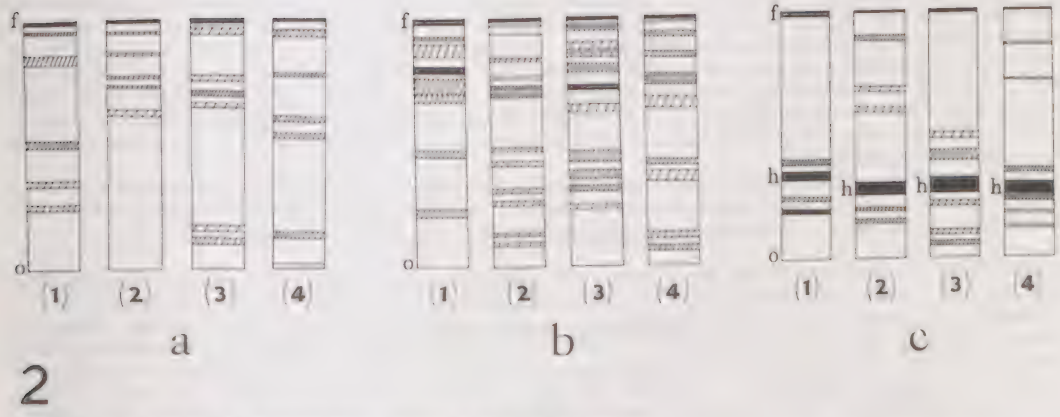

FIG. 1. Genitalia of (a) *Helicigona banatica* and (b) *H. hessei*.

FIG. 2. Electrophoretic patterns of (a) nonspecific muscle esterases, (b) nonspecific intestine esterases and (c) haemolymph proteins of (1) *Helicigona banatica*, (2) *H. maeotica*, (3) *H. arbustorum* and (4) *H. hessei*. f marks the front and the last esterase or protein band; o marks the origin; h indicates the haemocyanin band.

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STATUS OF *LAMELLIDEA SOLOMONENSIS* DELL (STYLOMMATOPHORA: ACHATINELLIDAE: LAMELLIDEINAE)[1]

Lamellidea pusilla (Gould)

1847 *Partula pusilla* Gould, *Proc. Bost. Soc. natur. Hist.*, 2: 197. Matea [Makatea].
1955 *Lamellidea solomonensis* Dell, *Pacif. Sci.*, 9(3): 357, fig. 1, a-d. Savo.
1958 *Tornatellina microstoma* Quadras & Moellendorff, Clench, *Natur. Hist. Rennell Is., Brit. Solomon Islands*, 2: 173. Santa Ana.
1959 *Lamellidea pusilla* (Gould), Solem, *Fieldiana* (Zoology), 43: 62. New Hebrides: Espiritu Santo. [Identified by Yoshio Kondo]
1960 *Lamellidea* (*Lamellidea*) *solomonensis* Dell, Cooke & Kondo, *Bernice P. Bishop Mus. Bull.* 221: 184. Savo.
1960 *Lamellidea* (*Lamellidea*) *pusilla* (Gould), Cooke & Kondo, *Bernice P. Bishop Mus. Bull.* 221: 184-193, figs. 81; 82, a-p; 83, a-e. Sixty-four islands in Polynesia, Micronesia and Melanesia.
1960 *Lamellidea pusilla* (Gould), Solem, *J. malacol. Soc. Austr.*, 4: 40. Solomon Islands: Florida. [Identified by Yoshio Kondo. Possibly *L. solomonensis* Dell: Solem]
1968 *Lamellidea* (*Lamellidea*) *solomonensis* Dell, Clench, *Natur. Hist. Rennell Is., Brit. Solomon Islands*, 5: 176. Rennell.
1972 *Lamellidea solomonensis* Dell, Turner & Clench, *Steenstrupia*, 2(15): 216. Savo.

Lamellidea pusilla is a small, slender, elongate-conic species with a sharply pointed apex, the dimensions centering around length 3.5 mm x width 1.75, whorls 5.5. Juveniles are equipped with vertically oriented palatal ribs, the upper edges of which are serrated (see Cooke & Kondo, 1960: 191, fig. 83). Eighteen adult and 16 juvenile *Lamellidea pusilla* were collected by me at Munda airstrip on New Georgia Island 160 miles northwest of Savo (Bishop Museum coll. no. 1966-175.4 and -175.5). Comparison of Dell's Savo *solomonensis* (Bishop Museum cat. no. 212365) with Solem's Florida Island *pusilla* (212382) and Kondo's Munda *pusilla* prove they are all *Lamellidea pusilla* (Gould). Dimensional comparison of the 3 are: Dell 2.5 x 1.5 mm, whorls 5 1/2 (subadult); Solem 3 x 1.9 mm, whorls 5 1/2; Kondo 3.3 x 2 mm, whorls 5 1/2.

On the face of it, Cooke & Kondo (1960: 184) appear to have accepted Dell's *solomonensis*, but such is not the case. It was inserted above *pusilla* in galley proof pending a future monograph of the genus *Lamellidea*, where it would have been synonymized with *pusilla*. The history of Dell's *solomonensis* is as follows: Dr. Dell wrote to me during the summer of 1953 requesting the determination of a species of *Lamellidea* from Savo. I was enrolled at Harvard Biological Laboratories for a 2-year Ph.D. program and therefore unable to help Dell since all the specimens were in Hawaii. Consequently, I advised Dell to publish his species. In 1955, Dell sent Bishop Museum 2 paratype specimens of his *solomonensis*, which I determined as *pusilla* and notated it for synonymy.

Cooke & Kondo's (1960) distributional map of *pusilla* and close allies (fig. 81, p 186) depicts a hollow in the southwestern sector. This hollow may now be filled to include Solomon and New Hebrides Islands; and New Britain, if Rensch's *microstoma* Quadras & Moellendorff is verifiable (Clench, 1958: 173).

LITERATURE CITED. — CLENCH, W. J. 1958. The land and freshwater Mollusca of Rennell Island, Solomon Islands. *Natur. Hist. Rennell Is., Brit. Solomon Islands*, 2: 155-202, pls. 16-19. — COOKE, C. M., Jr. & KONDO, Y. 1960. Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). *Bernice P. Bishop Mus. Bull.* 221: 1-303. — DELL, R. K. 1955. A tornatellinid land mollusk from the Solomon Islands. *Pacif. Sci.*, 9: 357-358. — GOULD, A. A. 1847. Descriptions of . . . species of *Partula*, *Pupa*, and *Balea*, collected by the Exploring Expedition. *Proc. Bost. Soc. natur. Hist.*, 2: 196-198. — SOLEM, A. 1959. Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana*, 43: 1-359. — SOLEM, A. 1960. Non-marine Mollusca from the Florida Islands, Solomon Islands. *J. malacol. Soc. Austr.*, 4: 39-56. — TURNER, R. D. & CLENCH, W. J. 1972. Land and freshwater Mollusca of Savo Island, Solomons, with anatomical descriptions (Mollusca, Gastropoda). *Steenstrupia*, 2(15): 207-232.

* * * *

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[1] Copies of the manuscript to this paper were sent to Dr. William J. Clench (Museum of Comparative Zoology, retired) and to Dr. R. K. Dell (Director, The National Museum of New Zealand at Wellington).

Proceedings of the

Society for Experimental and Descriptive Malacology

1974

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MOLLUSK SEMINAR

The University of Michigan
Ann Arbor, Michigan
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22 June, 1974

Malacological Review, 1975, 8: 115-128

PROGRAM

Convener, J. B. BURCH

Morning Session

Scanning electron microscope studies of the shell apices of freshwater limpets. J. B. BURCH

Scanning electron microscope study of radular teeth of *Physa gyrina hildrethiana* (Basommatophora: Physidae). George A. TE and A. John MARDINLY

Current taxonomic studies on the family Physidae. George A. TE

How fast is a snail's pace? Active and passive dispersal of *Physa integra* in Douglas Lake, Michigan. Philip T. CLAMPITT

Snail host-specificity of the nonhuman schistosome, *Gigantobilharzia huronensis* Najim 1950. Harold J. SAUER, Bernard GONIK and Harvey D. BLANKESPOOR

Cultivating *Fossaria bulimoides* (Lea), a snail host of the liver fluke, *Fasciola hepatica*. Yung-san LIANG and Henry VAN DER SCHALIE

Afternoon Session

A summary of studies on food and feeding in some European land snails. June E. CHATFIELD

Some observations on gastrulation of the gastropod *Ilyanassa*. Michael CRAIG

DDT in terrestrial slugs. Karl-Hans WURZINGER

Electrophoresis of *Stagnicola elodes* hemolymph. Paul H. RUDOLPH

Esterase patterns of some diploid *Bulinus* populations. Gene K. LINDSAY and J. B. BURCH

Systematic studies on the genus *Bulinus* from Algeria. Philip T. LoVERDE, Kamel ADDADI and J. B. BURCH

A new approach to the systematics and ecology of the genus *Cerion*. David S. WOODRUFF

SCANNING ELECTRON MICROSCOPE STUDIES OF THE SHELL APICES OF FRESHWATER LIMPETS[1, 2]

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Abstract

Apical shell sculpture has been important in delineating several of the generic groups in the freshwater limpet family Ancylidae (Walker, 1903, *Nautilus*, 17(2): 13-18; (3): 25-31; 1912, *Ibid.*, 25(12): 139-144; Pilsbry, 1913, *Proc. Acad. natur. Sci. Philad.*, 65: 618; 1924, *Ibid.*, 76: 49-66). Because of the greater resolution afforded by the scanning electron microscope (SEM) in studying surface details of minute objects, a SEM was employed for a closer, more detailed look at ancylid shell apex microsculpture. A number of species from various nominal generic taxa have now been examined: *Ancylus fluviatilis* Müller, *A. scalariformis* Stanković & Radoman, *A. tapirulus* Polinski, *Burnupia capensis* Walker, *B. gordonensis* (Melville & Ponsonby), *B. stenochorias* (Melville & Ponsonby), *Ferrissia cawstoni* Walker, *F. rivularis* (Say), *F. shimeki* (Pilsbry), *F. walkeri* (Pilsbry & Ferriss), *"Gundlachia" californica* Rowell, *"G." burnupi* Walker, *"G." l'hotellerieri* Walker, *Hebetancylus excentricus* (Morelet), *Laevapex diaphanus* (Haldeman), *L. fuscus* (Adams), *Rhodacmea filosa* (Conrad), *R. rhodacme* Walker and *Uncancylus concentricus* (Orbigny). These species exhibit 5 basic types of apical shell sculpture, which are described below.

I. *Ancylus, Rhodacmea.* (Figs. 1, 2). In these 2 genera the apical shell sculpture consists of radial ridges or cords which radiate distally to the juncture between the embryonic and post-embryonic shells, and may or may not (depending on the species) continue on the neanic shell and run to the apertural edge of the shell. The exact center of the apex is nearly smooth except for a pit, which seems to be characteristic of all freshwater limpets. But the apical tip of these 2 genera alone has a "dimpled" or "pushed-in" appearance.

In spite of the aberrant shells of Lake Ohrid *Ancylus*, the apical sculpture is the basic *Ancylus* type. The nearly identical apical sculpture of the shells of *Ancylus* and *Rhodacmea* is further evidence that these 2 genera are probably more closely related than many workers have suspected in the past.

II. *Ferrissia, "Gundlachia".* (Fig. 3). The apex of our specimens representing these 2 taxa were also radially striate, but in contrast to *Ancylus* and *Rhodacmea*, the striae are the result of radiating narrow grooves rather than raised cords. The incised grooves end abruptly at the termination of the embryonic shell. [The type species of *Gundlachia* Pfeiffer 1849 is *G. ancyliformis* Pfeiffer 1849, described from septate specimens, which are most likely ecologically conditioned shell abnormalities. Subsequently, all septate ancylid species have been assigned to *Gundlachia*, but most of them undoubtedly have closer affinities to *Ferrissia* than to *G. ancyliformis*. I have not had the opportunity to study *G. ancyliformis*, but Harry & Hubendick (1964, *Med. Göteborg., Mus. Zool., Avdeln*, 136: 1-77) consider *Hebetancylus* to be a synonym of true *Gundlachia*.]

III. *Laevapex, Hebetancylus.* (Fig. 4). With the light microscope the apex of our specimens appeared smooth, as previously described, but at higher magnification with the SEM can be seen an apical area of faint, very shallow, radiating ridges and grooves. This sculpturing is very weak, hardly visible, and is perhaps the degeneration of a once stronger sculpture in ancestral forms. [The species of *"Hebetancylus"* that I studied was Morelet's (1851, *Testacea novissima insulae Cubanae et Americae centralis*. Pars 2. J. B. Bailliére, Paris. 30 p) *Ancylus excentricus*, assigned to Pilsbry's (1913, *op. cit.*) genus *Hebetancylus* (type species: *A. moricandi* Morelet) following Basch (1963, *Bull. Mus. comp. Zool., Harvard*, 129(8): 401-461). However, before the above type of apex can be definitely used to characterize *Hebetancylus*, *H. moricandi* must be studied.]

IV. *Uncancylus.* (Fig. 5). The upper portion of the apex is nearly smooth, except for some nearly obsolete radial striae. The lower portion of the apex is densely but irregularly pitted, the rather shallow pits terminating at the end of the embryonic shell.

V. *Burnupia.* (Fig. 6). The apex of species of this genus is also characterized by pits, but of a quite different nature than those of *Uncancylus*. The apical pits of *Burnupia* cover the entire embryonic shell, except for the initial central smooth area at the tip of the apex. The pits have a very regular radial arrangement, and are generally deeper and are square or rectangular in shape.

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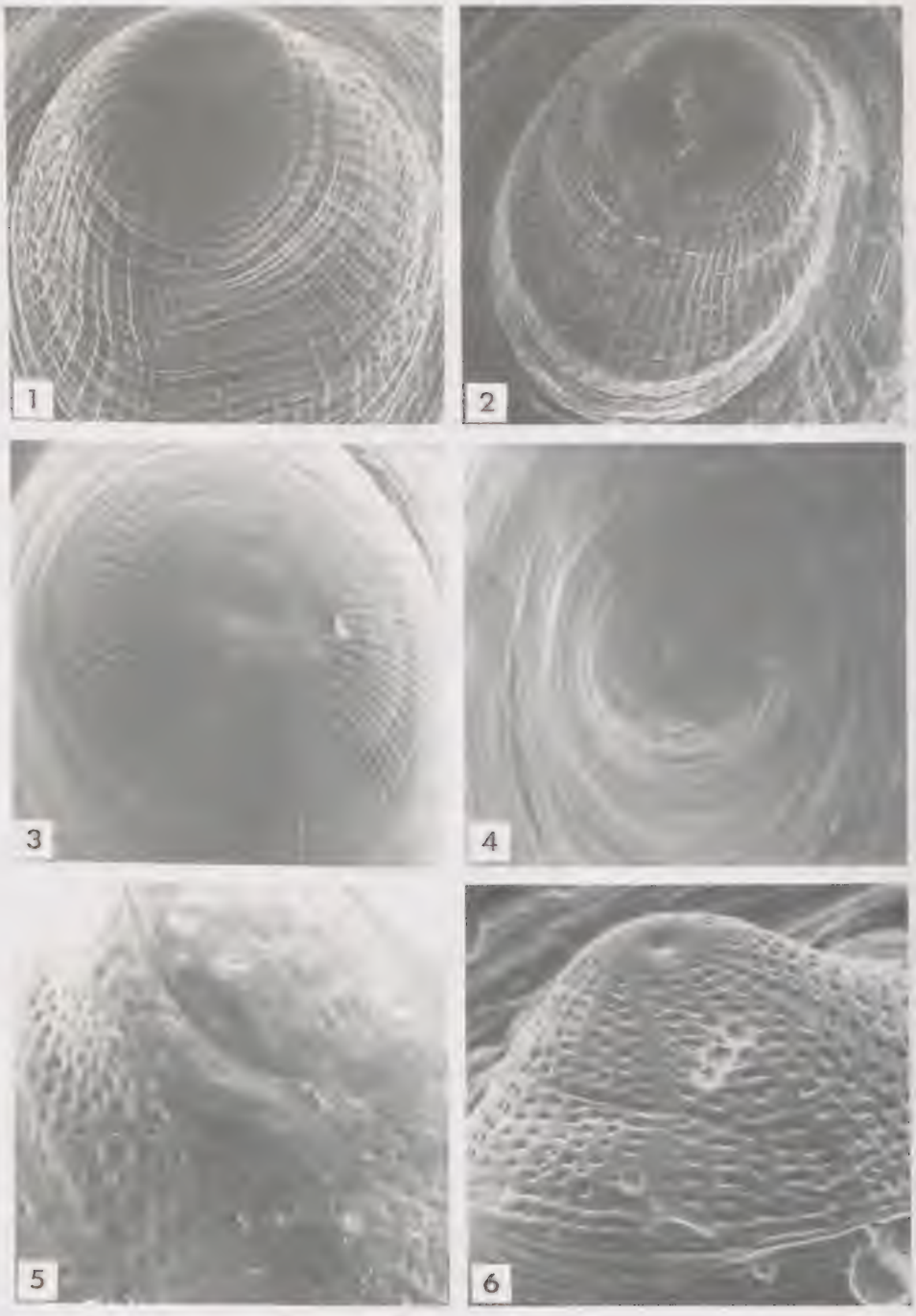
[2] Published *in extensio* (in part) in *Occasional Papers on Mollusks*, Harvard University, 4(50): 39-49, and (in part) in *Malacol. Rev.*, 7(2): 127-132.



FIGS. 1-6. Apical microsculpture of ancylid shells. FIG. 1. *Ancylus fluviatilis*, Ohrid, Yugoslavia. FIG. 2. *Rhodacmea filosa*, Tallaseehatchee Creek, Talladega Co., Alabama. FIG. 3. *Ferrissia cawstoni*, Avoca, Natal, South Africa. FIG. 4. *Laevapex fuscus*, Miami River, Ohio. FIG. 5. *Uncancylus concentricus*, Brasil. FIG. 6. *Burnupia capensis*, Escomba, Natal, South Africa. Figs. 1, 2, 4 - x65; Fig. 3 - x140; Fig. 5 - x195; Fig. 6 - x130.

SCANNING ELECTRON MICROSCOPE STUDY OF RADULAR TEETH OF *PHYSA GYRINA HILDRETHIANA* (BASOMMATOPHORA: PHYSIDAE)

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Abstract

The following description of the radular teeth of a single specimen of *Physa gyrina hildrethiana* (from Ann Arbor, Michigan) as seen through the scanning electron microscope (SEM) establishes a baseline for a comparative family-wide survey of radular dentition. The procedure used was as follows. The radula was glued to an aluminum stub with Duco cement and coated with a 100 Å thickness of gold using a glow discharge coater. The microscope used was a modified JEOL model-JSM-U3 scanning electron microscope. The specimens were examined with secondary electron imaging using 15 kv accelerating voltage.

In this specimen, the central tooth and the 1st lateral tooth are both very distinct. The central tooth has a single large central cusp with 3-4 small cusps on each side (Fig. 1). The 1st lateral tooth has 4-5 large cusps alternating with 1 small cusp per large cusp (Fig. 2). The rest of the teeth show a very gradual transition from those with a single small cusp alternating with large cusps, to those with 3 small cusps alternating with large cusps. A transition zone occurs approximately at the 20th to 30th teeth (Fig. 3). From the 30th tooth on, teeth with 3 small cusps alternating with large cusps occur more regularly (Fig. 4).

The smaller cusps are often not seen with the light microscope, and therefore many of the radular studies done by earlier workers are obsolete.

FIGS. 1-2. SEM photomicrographs of radular teeth of *Physa gyrina hildrethiana*. Arrows point to the particular teeth mentioned in the following figure legends. FIG. 1. Central tooth (ca. x 3050). FIG. 2. First lateral teeth (ca. x 2250).

FIGS. 3-4. SEM photomicrographs of radular teeth of *Physa gyrina hildrethiana*. Arrows point to the particular teeth mentioned in the following figure legends. FIG. 3. Twentieth to 22nd teeth, showing the transition zone between the lateral and marginal teeth (ca. x 2760). FIG. 4. Fiftieth and 51st teeth (ca. x 2550).

CURRENT TAXONOMIC STUDIES ON THE FAMILY PHYSIDAE

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Abstract

The nature of earlier taxonomic systems in the family Physidae has been reviewed; these systems are low in information content, typological in orientation and heavily dependent on a limited set of shell characters. These are some of the major reasons for the traditional impasse in species identification, as well as in systematic and evolutionary understanding of this family. In order to break this impasse, new approaches need to be taken, and a reorientation from a typological to a dynamic species concept is necessary. In making taxonomic assessments, sample sizes of shells, preserved animals and live animal populations have to be increased, as well as the number of characters and character states used. Taxonomic clarity and stability are seen here as a direct function of increase in information contents.

Toward this eventual goal of family revision, I have screened over 20,000 shell lots from 7 museums. Initially, a conchological species delineation was instituted with the 7000 lots of physid shells housed in the Museum of Zoology, The University of Michigan (UMMZ). Species delineations were based on continuity and discontinuity in shell series, taking into consideration an extensive pool of type specimens from various museums. The goal here was to search for taxonomic "gaps"; these gaps were then taken to be equivalent to species-gaps. Globally, the Physidae exhibit 46 such gaps. This 1st hypothesis on species delineation was then tested with the 3000 lots of shells lodged at the Academy of Natural Sciences of Philadelphia (ANSP) and proven correct. Screening from other museums shows that both the ANSP and UMMZ physid collections are representative of those found in other museums. The hypothesis therefore was not drawn from a biased sample.

The next step was to build an inventory of alcohol-preserved specimens and live populations. To date, 962 lots in alcohol have been accumulated representing diverse conchological characteristics and geographic origins, and 55 field populations representing 20 species are being maintained in aquaria. With identities of alcohol-preserved and live specimens tied to the conchologically "valid" species names, a step-by-step species evaluation can now begin.

A search for shell, anatomical and live morphological characters and character states has begun. The number of useful conchological characters was increased from the less than 10 traditionally used to 29 characters. Anatomical characters were expanded from the previous dual emphasis on mantle digitation and the penial complex to include the kidney, mantle border and spermatheca. The penial complex was partitioned into 9 analyzable components. Live morphological characters, very much ignored in previous literature,

were found to be very useful (e.g., shape of oral lappets, shape of the posterior foot, type of tentacles, mantle color patterns, etc.). Live material can also be subjected to electrophoretic and serological procedures, and initial studies along these lines have already been undertaken. The radula, previously supposed in some literature to be meaningless due to high variability, was found, on the contrary, to be potentially important for grouping species. This was determined by the use of scanning electron microscopy techniques, which expose in clear view the smaller denticles previously not seen, or variably seen, with the light microscope.

At present, the various characters and character states have started to fall into definite patterns; also, new data reinforce old data. This indicates that a definite plateau has been reached and that the 1st systematic synthesis is now in order. From all indications, the data show that a taxonomic revision can be made and, further, that a phylogenetic hypothesis for the family Physidae can be developed.

With so much data on hand, there is a danger of unconsciously leaning toward one particular set of characters as opposed to another set. This is inherent in the whole issue of "character weighing". In order to prevent inordinate biases in evaluating characters, I am currently investigating numerical taxonomic procedures in order to complement the systematic analysis.

HOW FAST IS A SNAIL'S PACE? ACTIVE AND PASSIVE DISPERSAL OF *PHYSA INTEGRA* IN DOUGLAS LAKE, MICHIGAN

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Abstract

Field data were collected on active dispersal in juveniles and passive dispersal in adults, of *Physa integra* Haldeman, a freshwater pulmonate snail living in Douglas Lake, Michigan, U.S.A. These data supplement work previously reported (Clampitt, 1974, *Amer. Midl. Natur.*, 92(2): 275-300) on seasonal migratory cycle and related movements in *P. integra*.

Quantitative sampling and field experiments with marked juvenile *Physa integra* in August 1973 revealed an active movement of these juveniles away from the "preferred" substratum of stones adjacent to shore and onto sand 10-15 m from shore. The fact that the juveniles found on the sand substratum were mostly larger (5-9 mm shell length) than those on the stones adjacent to shore (2-7 mm, 4.5 mm avg. shell length) suggests that this summer migration away from shore was at least in part a function of age and shell size. The field experiments with larger (7-9 mm) marked juveniles revealed that, although most snails moved considerably less than 5 m away from shore within 24 hours after release, and well under 10 m in 5 days, at least 1 had moved 10 m within the first 12 hours. These data together reveal that, although the trend of movement by the juveniles at this season is opposite that of the parent generation in spring and early summer (see Clampitt, 1974, *op. cit.*), the rates of active dispersal of the juvenile and adult generations are very comparable.

Field experiments with marked adult *Physa integra*, released in June 1972 on a wave-swept sandy shoal (the "Big Shoal") at the east end of Douglas Lake, in water 0.5 m deep and 20 m from shore, revealed a remarkable amount of passive dispersal of the snails by wave action and currents. After one 24-hour period, including several hours of strong and steady northwest wind which created considerable wave action and a definite north to south current parallel to shore, 227 living (and 2 dead) snails were recovered (of 400 released initially); 3 of these were clinging to a wooden stake which marked the center of the release area, and 41 others were found within 20 m downwind from release; the other 183 living snails were all carried downwind (south) also, mostly between 20 and 40 m from release, although 2 had been carried nearly 60 m. Nearly all of the recovered snails were found within a narrow strip between 10 and 25 m from shore. A similar experiment, lasting for 7 days and including an unusual 4-day period of strong and steady northerly winds, yielded even more dramatic results; of 92 living (and 12 dead) snails recovered (from the 400 initially released), 59 living (and 5 dead) snails were found between 50 and 240 m downwind from release; 1 living snail was 225 m from the release point. Again, nearly all snails recovered were between 10 and 25 m from shore. Not only are these data remarkable in themselves, but they help to illustrate the severity and instability of this exposed environment, and the rather remarkable tolerance of *P. integra* - at least temporarily - to such conditions.

The dramatic contrasts in active and passive dispersal rates, under field conditions, between *Physa integra* and the much more sedentary, burrowing, non-migratory planorbid snail, *Helisoma anceps* (Clampitt, 1972, *Malacol. Rev.*, 5: 11-12; 1973, *Malacologia*, 12(2): 379-399; and unpubl. data), illustrate the fact that "a snail's pace" varies greatly depending on the species. Available evidence suggests that many species of the family Physidae disperse actively and rapidly, while at least some members of the family Planorbidae (*H. anceps* and *H. campanulata* among them) move very little for weeks or months at a time.

SNAIL HOST-SPECIFICITY OF THE NONHUMAN SCHISTOSOME, *GIGANTOBILHARZIA HURONENSIS* NAJIM 1950[1]

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Abstract

Eggs of the trematode, *Gigantobilharzia huronensis* Najim 1950, were collected from feces of experimentally infected passerine birds. After hatching, the miracidia were introduced to young snails (2-3 mm) of the following species: *Physa gyrina, Physa halei, Physa heterostropha, Physa integra, Physa parkeri, Physa virgata* and *Lymnaea stagnalis*. Temperature, light, age of miracidia, length of exposure, size and age of snails were kept constant during this investigation.

At post-exposure day 17, snails were individually isolated, placed under fluorescent light for 2 hours and then examined for emerging cercariae. Five weeks later (day 52) this shedding procedure was repeated. Because cercariae of *Gigantobilharzia huronensis* show diurnal periodicity, tanks containing exposed snails were covered earlier with black cloth to prevent premature shedding.

Highest infections (48-80%) were in *Physa gyrina, P. integra* and *P. parkeri*, which were exposed to 2 miracidia each. However, other snails of both *P. gyrina* and *P. integra*, exposed to 1 miracidium each, had correspondingly lower infections. A much lower infection rate (less than 3%) was found in *P. heterostropha*, exposed to 2 miracidia. None of the *P. halei, P. virgata* or *Lymnaea stagnalis* became patent during the course of these experiments.

Mortality of infected *Physa integra* and *P. parkeri* between days 17 and 52 was very high. These deaths may be attributable to the avian blood flukes, e.g., in *P. parkeri* the percentage of infection dropped from 76 to 14 between days 17 and 52, with a 72% mortality within the same 5-week period. In *P. integra* the reduction was even more drastic because the infection dropped from 80% to 2% with a 70% mortality. Among the other species, mortality ranged from 0-14% during the same period. Previous work with this life cycle indicated that a normal snail host, *P. gyrina*, does not usually tolerate more than 1 miracidium and, consequently, the death rate even in these relatively low-level infections was very high. It was so striking that the assumption was previously made that this normal *Physa* host would not survive if given more than a single miracidium.

This preliminary study suggests that *Gigantobilharzia huronensis* exhibits a low degree of snail host-specificity. Among the species of gastropods tested, the best experimental hosts for this avian blood fluke are *Physa gyrina, P. integra* and *P. parkeri*. Of these 3, *P. gyrina* seems to be the best host species because of its much lower mortality rate. Our field data support this conclusion.

Host-specificity studies, such as *Gigantobilharzia huronensis* in various physids, could prove useful in delineation of species within gastropod genera. Such studies may also suggest biochemical and structural similarities or differences in related species. Furthermore, there appears to be a positive correlation between the distribution of physids known to be capable of experimentally harboring *G. huronensis* and the incidence of "swimmer's itch" in the Midwest. The physiological host-parasite relations as may exist could be reflected in the distribution of the snails tested. The 3 species of *Physa* (*P. gyrina, P. integra* and *P. parkeri*) that were the most suitable hosts all have distributional ranges within the Great Lakes region in which *Gigantobilharzia huronensis* normally occurs. The ranges of *P. halei, P. heterostropha* and *P. virgata* are rather removed from those of the 3 species that were susceptible; *P. halei* is common to Missouri and south through Alabama and Texas; *P. heterostropha* is a northeastern species and *P. virgata* is a southwestern species and is known to occur in Texas, Arizona, Utah and west to California. Little or no information is available to indicate that *Gigantobilharzia* occurs beyond the Great Lakes region, and even within that area little is known about its precise range.

[1]Supported (in part) by The Rockefeller Foundation (Medical Malacology) under Grant No. GA HS 7424 and (in part) by the U.S. Army Medical Research and Development Command, Washington, D.C. 20314 under Contract/Grant No. Army DA-49-193-MD-2651.

CULTIVATING *FOSSARIA BULIMOIDES* (LEA), A SNAIL HOST OF THE LIVER FLUKE, *FASCIOLA HEPATICA*[1]

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Abstract

Although *Fossaria bulimoides* (Lea) and its forms (*F. b. cockerelli* (Pilsbry & Ferriss) and *F. b. techella* (Haldeman)) are distributed widely in the western United States, information on culturing this important snail is difficult to find. Recent algal culture methods developed by Liang (1974, *Sterkiana*, (53): 7-52; (54): 1-27) were useful in culturing it. Basic information on survivorship, fecundity and growth was obtained from 40 newly hatched snails obtained from 2 egg masses and placed in Petri dishes. Cultures were renewed twice a week until all snails died. Survivorship was excellent; by the 4th week most snails produced eggs. Unlike *Biomphalaria* and *Bulinus*, which exhibit more or less continuous growth until death, *F. bulimoides* stopped growing at about 13.5 mm after the 15th week. Half the population died at 15 weeks; the longest life span was 25 weeks. Egg-production continued for a long period (1-20 weeks); once stopped, it did not resume. About half the population ceased ovipositing at 10 weeks; total eggs laid by 1 snail ranged from 38 to 6,780; the largest number of eggs laid by an individual in 1 week was 1,038.

Crowding was measured using newly hatched snails derived from a single parent and reared in 12 Petri dishes. During an 8-week period, growth was best in Petri dishes with 1 snail per dish; egg-laying was best in dishes with 5 snails (1,004 eggs per snail in 8 weeks). Three types of cultures were tested for 8 weeks: growth was best (snails attaining an average of 10.1 mm shell length) in tall Petri dishes; least (averaging only 8.9 mm shell length) in regular Petri dishes; total eggs laid per snail was best in tall Petri dishes (1,168 eggs) and in trays (1,163 eggs).

[1] This work was supported by the U.S. Army Medical Research and Development Command, Washington, D.C. 20314, under Contract/Grant No. Army DA-49-193-MD-2651.

A SUMMARY OF STUDIES ON FOOD AND FEEDING IN SOME EUROPEAN LAND SNAILS[1]

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Abstract

Although there are some references to the food of slugs and snails, many simple facts relating to the food taken and how this varies from place to place and from season to season are unknown in any detail, in spite of the economic interest in slug research. The larger snails and slugs have received the most attention (Frömming, 1962, *Das Verhalten unserer Schnecken zu den Pflanzen ihrer Umgebung*. Duncker & Humblot, Berlin. 348 p; Grime & Blythe, 1969, *J. Ecol.*, 57: 45-66; Grime, MacPherson-Stewart & Dearman, 1968, *J. Ecol.*, 56: 405-420). The smaller species have been less studied, although many of them are common and numerically quite important in the ecosystem (Mason, 1970, *Oecologia*, 4: 358-373; 5: 215-239).

My investigations on feeding in land snails were done primarily in southeast England and involved the helicid snails *Monacha cantiana* (Montagu) and *Hygromia striolata* (Pfeiffer); *M. cartusiana* (Müller) was studied in France. Other investigations with a former colleague have been done on the common endodontid snail *Discus rotundatus* (Müller), again from southeast England. The populations of *M. cantiana* and *H. striolata* studied were mostly from roadside stinging nettle patches in the county of Berkshire, while the populations of *M. cartusiana* were from grassy roadside banks in the vicinity of Poitiers and in the Dordogne region of France (Chatfield, 1968, *Proc. malacol. Soc. Lond.*, 38: 233-245; 1972, *Ibid.*, 40: 59-69). The population of *D. rotundatus* was from a scree in an old chalk cutting near Portsmouth, U.K., which was colonised by deciduous trees and shrubs (Barrett & Chatfield, 1973, *J. Conchol.*, 28: 13-21).

The food materials of the snails were established by the examination of the gut contents and faecal strings which were studied at different months of the year. After fixing in alcohol, temporary mounts were made in Berlese Fluid for examination under the microscope. The plant fragments were identified where possible, using the detailed structure of plant hairs, vein patterns, type and arrangement of stomata and the shapes and arrangements of epidermal cells. The plant fragments from the gut contents and faeces of snails were compared with standard mounts of identified plants from the same habitat. A summary of results is shown in Table 1.

TABLE 1. A summary of food plants detected in gut contents or faecal strings of the snails studied in this investigation.[1]

Snail	Locality	Habitat	Food plants															
			Urtica dioica	*Lamium album*	*Anthriscus sylvestris*	*Heracleum sphondylium*	*Cirsium arvense*	*Glechoma hederacea*	*Mercurialis perennis*	*Fagus sylvatica*	Dicotyledons undeter.	*Dactylis glomerata*	*Brachypodium pinnatum*	Grass	Fungal hyphae	Flower petals	Algae
Helicidae																		
Monacha cantiana	Play Hatch, Berkshire	Roadside	+	+	+	+	+	-	-	-	+	+	+	+	+	-	-
	Play Hatch, Berkshire	Field	-	+	-	-	-	+	-	-	-	-	-	+	+	-	-
	Southridge, Berkshire	Nettle bank	+	+	+	+	+	?	-	-	-	-	-	+	+	-	-
	Ridgeway, Berkshire	Chalk grassland	-	-	-	-	-	-	-	-	+	-	+	+	+	-	-
	St. Vaast, N. France	Roadside	-	+	+	-	-	+	-	-	+	-	+	+	-	+	-
Monacha cartusiana	Pouzioux, nr. Poitiers, France	Grass bank	-	-	-	-	-	-	-	-	+	-	+	+	+	-	-
	Thenon, Dordogne, France	Grassland	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-
	Nogent, France	Roadside bank	-	-	-	+	-	-	-	-	+	+	-	+	-	-	-
Hygromia striolata	Play Hatch, Berkshire	Roadside	+	+	-	-	-	+	-	-	+	-	-	-	+	-	-
	Norbury Park, Surrey	Woodland	-	-	-	-	-	-	+	+	-	-	-	-	+	-	-
	Juniper Hall, Surrey	Base of wall	-	-	-	-	-	-	-	+	+	-	-	+	+	-	-
Endodontidae																		
Discus rotundatus	Portsdown Hill, Hampshire	Wooded quarry	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+

[1] All specimens were collected in the U. K. except *Monacha cartusiana* and 1 sample of *Monacha cantiana* collected in France.

From the results it is evident that there was some overlap in the feeding of *Monacha cantiana* and *Hygromia striolata* when they were living together in the same habitat at Play Hatch. Stinging nettles, *Urtica dioica* Linnaeus, were one of the major food plants of these 2 snails at Play Hatch and Southridge, Berkshire. The major difference between *M. cantiana* and *H. striolata* was that only *H. striolata* would penetrate into woodland where it would also feed. Evidence of this was the fragments of beech leaves (*Fagus sylvatica* Linnaeus) and leaf fragments of the woodland herb *Mercurialis perennis* Linnaeus which were recorded from gut contents and faeces of *Hygromia*. Examination of gut contents and faeces of *M. cartusiana* collected from grassy banks showed that grass formed the bulk of the food, whether in a fresh state or brown and decayed. In most situations in which high density populations of helicid snails were studied, the most frequent food plants found in gut or faecal contents were usually the common ones in the plant community. There was evidence

that stems, leaves and flowers were rasped by the snails. Fungal hyphae, usually associated with decaying plant material, were present in the gut contents of the snails studied.

As the 3 helicid snails were fairly large (8-18 mm shell diameter), the food fragments were of a reasonable size for identification (up to 5 mm in length). A comparative study of the smaller endodontid snail *Discus rotundatus*, which has a flatter shell and usually grows to a maximum of 6 mm shell diameter, showed that this snail could only ingest small fragments of food. On account of their size and often the greater stage of plant decay, these were more difficult to identify. Investigations on the feeding of *D. rotundatus* showed that green algae (of the Order Chlorococcales), which grew on moist pieces of chalk in the scree, was one of the most important foods of this snail in that habitat. After feeding on algal chalk, *Discus* produced green faecal strings and microscopic examination confirmed the presence of algae. In addition to algae, some fungal hyphae were recorded from the faeces of *D. rotundatus*. *Discus* was thus behaving as a microphagous rather than a macrophagous feeder.

Field work at different times of the year showed that the feeding habits of *Monacha cantiana* and *Hygromia striolata* were affected by the seasons. In winter most of the faeces of these 2 snails were brown in colour, whilst in the summer a high proportion of the faecal strings were green. Detailed examination of the faecal material mounted in Berlese Fluid showed a higher proportion of stem fragments compared with leaf fragments in the winter months. Most of the plants in the habitats studied died down in winter, particularly the stinging nettle (*Urtica dioica*) and cow parsley (*Anthriscus sylvestris* (Linnaeus) Hoffmann), which dominated the vegetation at other times of the year. Thus, in winter, the dead stems of the previous summer's growth were the only food easily available to the snails. As spring progressed, more leaf fragments were present in the gut contents of the snails, firstly *Anthriscus* as the major food plant (March) and later *Urtica* (June). The percentage of the various food plants represented in gut contents and faeces of *Monacha* and *Hygromia* was closely related to their availability in the habitat.

The British winter shows considerable variation in temperature (Chatfield, 1968, *op. cit.*). During fairly warm periods with minimum temperatures several degrees above freezing, both *Monacha cantiana* and *Hygromia striolata* may continue to be active and to feed (as evidenced by food in the gut). However, little growth takes place in *Monacha* during the winter (Chatfield, 1968, *op. cit.*), and this is probably partly due to the low nutritional quality of the food which is eaten (dead stem material), as well as to the effect of the lower winter temperature on the metabolism of snails. During weather with temperatures around the freezing point and below, *M. cantiana* was recorded at ground level situated with the aperture of the shell uppermost and sealed by a thin epiphragm. Samples of *M. cantiana* which were collected during frosty weather and dissected showed an empty gut in almost every snail.

Temperature, in addition to inhibiting growth in winter, can regulate the rate of growth during spring and summer. In some preliminary experiments on feeding *Discus rotundatus* on algae, different rates of shell growth can be explained in terms of temperature (Barrett & Chatfield, 1973, *op. cit.*). Snails kept in a temperature range of 10-21°C grew at almost half the rate of those kept in a temperature range of 15-27°C. In both cases similar numbers of snails were used in similar containers and they were given an excess supply of algal chalk.

In summary, the field work basis of this project has shown the great seasonal variability in the habitat in terms of temperature (and its effect on metabolism) and the types of food materials available. In a terrestrial ecosystem (more variable in climate than an aquatic one), the rate of growth of snails in the field tends to reflect weather conditions. Laboratory work and experiments proved helpful in analysis of faecal material and in testing hypotheses. More detailed studies on feeding and growth rates of *Discus rotundatus* are being continued in the Portsmouth area, U.K., by B. W. Barrett.

[1]I am grateful to Dr. Vera Fretter of the University of Reading for her guidance during my work on the helicid snails, and later for her interest in our investigations of *Discus rotundatus*. Thanks are due to Dr. A. E. Round for identifying the alga.

SOME OBSERVATIONS ON GASTRULATION OF THE GASTROPOD *ILYANASSA*[1]

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Abstract

Despite the common occurrence of the epibolic gastrulation pattern in the Gastropoda, little is known about it. Embryos of the marine prosobranch *Ilyanassa obsoleta* demonstrate this pattern and are currently under investigation. The eggs from a single capsule were removed in filtered, pasteurized sea water (PSW), washed several times in PSW, allowed to attain trefoil, then placed in an incubator at 20°C. At a specific stage of development, i.e., at 30 minutes following the formation of the 1st quartet, at 30 minutes following

the formation of the 2nd quartet, and at 18 hours, 24 hours, 32 hours and 40 hours post-trefoil, the embryos from a single capsule were divided into equal aliquots; one aliquot was placed into 5 ml of 2 µg/ml cytochalasin B (1 mg/ml DMSO, stock) and the other aliquot into 5 ml of 0.2% DMSO in PSW as a control. The embryos were allowed to incubate in these solutions at 20°C until the controls completed gastrulation at approximately 48-50 hours of development post-trefoil. The experiments were monitored visually and photographed.

Embryos incubated in cytochalasin B during the 1st quartet failed to gastrulate and remained permanently arrested at the 1st quartet. After 5 hours of incubation, the micromeres and macromeres were extremely spherical and maintained only minimal areas of contact with each other; this blastomere dissociation continued to 50 hours, at which time the embryos that remained undissociated exhibited blastomeres that were collapsed upon one another. Like those of the 1st quartet, the embryos incubated in the drug during the 2nd quartet also failed to gastrulate, and they remained permanently arrested at the 2nd quartet. Incubation in the drug at 18 hours, 24 hours, 32 hours and 40 hours post-trefoil produced embryos which were arrested and failed to gastrulate, but the percentage of defective embryos decreased with increasing developmental age post-trefoil. Embryos incubated in cytochalasin B at 18 hours demonstrated an array of spherical, nonconfluent micromeres spread over the surface of the animal pole region but not enveloping the A-, B-, or C-quadrant macromeres completely. When cytochalasin B was applied to 24-hour embryos, micromeres at and near the leading edge became very spherical, and, subsequently, the leading edge became rounded and regressed towards the animal pole, exposing the macromeres of the A, B, and C quadrants. Simultaneously, the whole animal pole flattened in many cases, and few spherical micromeres were seen in this region. Leading edge regression was also observed in treated 32- and 40-hour embryos. In 32-hour embryos, the extent of regression varied, the most severe examples having an appearance similar to treated 24-hour embryos; however, unlike the 24-hour embryos, most treated 32-hour embryos demonstrated spherical micromeres only at the leading micromere edge, the rest of the micromere layer being uniformly confluent and having a normal appearance. Like the 32-hour embryos, 40-hour embryos demonstrated variations in micromere regression, but even in the most acute examples, only the surface of D was uncovered and not that of the other macromeres; in these treated embryos, isolated spherical micromeres may appear at other loci over the micromere field as well as at the leading edge.

These results seem to indicate that continuing cleavage is necessary for normal epiboly. Leading edge micromere spherulation and regression also indicate that the leading edge micromeres become important in the progression of the edge.

[1]Supported, in part, by a grant from the University of Michigan Cancer Research Institute.

ESTERASE PATTERNS OF SOME DIPLOID *BULINUS* POPULATIONS[1]

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Abstract

Bulinus, a genus of freshwater pulmonate snails found chiefly in Africa, has received notoriety and much attention because some of its species transmit *Schistosoma haematobium*. In previous studies we have shown: 1) that polyploidy occurs in the *tropicus-truncatus* species group; 2) that morphologically the species of the diploid-polyploid species complex are rather uniform; and 3) that in this particular group of species, those species that are responsible for transmission of schistosomiasis are tetraploid, i.e., they have twice the normal complement of chromosomes; but 4) even in the normal diploid refractive group of species, several populations have a limited susceptibility to schistosome infection, thereby indicating the possibility of individual and population physiological variability. However, there is very little information about population or individual variability regarding various physiological/biochemical parameters, and as a preliminary survey we decided to test for variability in non-specific esterases in various of our inbred laboratory populations. We believe that studies such as these on a wide range of populations, especially field populations, will be valuable in studying inter- and intra-populations polymorphism, which may possibly be correlated with susceptibility to parasite infection.

The standard disc gel electrophoretic technique as previously employed in our laboratory was not sensitive enough to apply to individual *Bulinus* specimens, so a new gel configuration was developed. Six to 8 mg of foot tissue from 1 snail was sonicated in 0.2 ml of physiological solution. The resulting homogenate was mixed with 0.4 ml of concentrated upper gel and centrifuged to remove any reticulate matter. This 0.6 ml of sample was then removed from the test tube and placed into an expanded sample volume at the top of the standard gel stack. Electrophoresis was performed at 5 ma/tube and the resulting separations were stained

for non-specific esterases. We took 12 large adult snails from each aquarium population and ran each individually, standardizing all procedures.

Observations: 1) Nine different esterases were separated from the 12 diploid populations; 2) these esterases showed a general distinctive pattern in the populations; 3) only 1 of the esterases (band A) occurred in all the individuals of all of the populations; 4) all individuals of some populations lacked certain bands, e.g., band C in one population from South Africa and one from Kenya, and band D from a Rhodesian population; 5) two populations from Rhodesia had an esterase not present in the other 10 populations - in all the individuals in one population and in 3 of the individuals in the other population; 6) the 2 populations partially susceptible to schistosome infection did not show any noticeable differences in esterases from the other 10 non-susceptible populations.

[1]Supported by grants from the Office of International Activities, Smithsonian Institution, and the Rockefeller Foundation (GA BMS 7215).

SYSTEMATIC STUDIES ON THE GENUS *BULINUS* FROM ALGERIA[1]

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Abstract

The African subgenus *Bulinus* is of medical importance because some of its species are the intermediate hosts for *Schistosoma haematobium*. In the *truncatus-tropicus* species group, parasitological differences have long been recognized, but the species constituting this group have proven difficult to define in more precise biological terms. The biological differences (parasitological, cytological, immunological and electrophoretic) have resulted in 2 main species groups being recognized, the *tropicus* and *truncatus* groups being of greatest medical importance.

In 1973, we initiated a program to study *Bulinus* in North Africa. The present report deals with *Bulinus* collected from Foundouk at the Barrage du Hamiz, Algeria, and the relationship of this population to the more thoroughly studied bulinine species in other parts of Africa, using cytological and biochemical and scanning electron microscope (SEM) techniques.

Our *Bulinus* population from Algeria is a tetraploid (n=36). Immuno-taxonomy using the micro-Ouchterlony technique (see Burch & Lindsay, 1970, *Malacol. Rev.*, 3: 1-18) shows "identity" of foot-muscle proteins with *Bulinus truncatus* (n=36) and "non-identity" with *Bulinus tropicus* (n=18). Determination of non-specific esterases from foot muscle showed a pattern identical to other *B. truncatus* populations studied. The radula (studied by SEM) is characteristic of a *B. truncatus* group species in having arrowhead shaped mesocones on the 1st lateral teeth.

The results based on modern taxonomic criteria show that the Algerian *Bulinus* collected from Foundouk at the Barrage du Hamiz belong to the *B. truncatus* species group. There is some immunological indication (presence of a spur in the "identity" reaction with *B. truncatus*) that the Algerian population may have undergone some divergence due to geographical isolation.

[1]Supported by research grants from the Smithsonian Institution (SF3-00110), the Rockefeller Foundation (GA BMS 7215) and the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service (N.I.H. Training Grant No. 5 T1 AI 60).

A NEW APPROACH TO THE SYSTEMATICS AND ECOLOGY OF THE GENUS *CERION*[1]

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Abstract

The West Indian pulmonates of the genus *Cerion* are remarkable for the extreme variability of their shells. The vast array of shell types present in Cuba and the Bahamas, coupled with past typological taxonomic practices, have resulted in the naming of over 600 "species". The complex patterns of geographic variation are so confusing that several workers have despaired at the possibility of ever applying the biological species concept to this group. The alleged haphazard distribution of shell types has been attributed to the vagarities of hurricane dispersal.

Gould (1969, *Syst. Zool.*, 18: 185-200; 1971, *Breviora*, (372): 1-26) began work on the *Cerion* of the Dutch Leeward Islands several years ago. Using powerful multivariate techniques to analyse the complex patterns of geographic variation, he demonstrated that phenotypic variation was continuous rather than capritious, and adaptive rather than adventitious. Since 1972 we have collaborated on a holistic study of the variation, ecology and evolution of these remarkable land snails throughout their range.

Commencing with the 9 extant taxa of the Little Bahama Bank islands, we have examined genetic and phenetic variation in over 2000 individual adults representing 55 populations. Gould has studied patterns of within and between population variation in 19 morphometric characters. I have surveyed variation in 28 enzymes using starch gel electrophoresis. Eighteen of these have given reproducible patterns that are interpretable genetically: phenotypic ratios (and presumed genotypic ratios) closely agree with Hardy-Weinberg expectations for large outbreeding populations. If my tentative genetic interpretations are correct, then on the basis of the 18 loci surveyed, *Cerion* has about 20% of its loci polymorphic per population. In one area the mean genic heterozygosity per individual (H) was 0.059 (range 0.053-0.068). Formal breeding experiments will be undertaken shortly to properly establish the genic basis of the allozyme variation patterns.

Our studies of variation are proving highly illuminating from a biosystematic point of view. For example, at Pongo Carpet on Great Abaco we discovered populations characterized by shells quite unlike those of *Cerion bendalli*, the only form known from the northern half of the island until now. On the basis of all previously employed criteria we should have described the variant populations as a new species. Electrophoretic studies of allozymic variation reveal, however, that the Pongo Carpet populations are genetically indistinguishable from *C. bendalli*. Furthermore, R-mode factor analysis of the patterns of covariance of major determinants of shell geometry show that the 2 groups are basically very similar. As a result of additional multivariate analyses we were able to show that the Pongo Carpet morphotypes are merely clinal variants of *C. bendalli* (Gould, Woodruff & Martin, *Syst. Zool.*, 23: 518-535).

A similar study of the 82 "species" of New Providence island (Nassau) is now in progress. As a result of these studies and others involving *Cerion* elsewhere in the Bahamas and Cuba, we anticipate a downward revision of the number of valid species of close to 2 orders of magnitude. Furthermore, while hurricanes may have played a role in establishing distribution patterns, their importance appears to have been overestimated. We can discern an overall biogeographic pattern (at least in the northern Bahamas) that appears to have evolved *in situ* during the late Cenozoic.

Despite the enormous taxonomic literature on *Cerion*, we know remarkably little about their natural history. It was widely held that the snails are obligate halophiles, that they are restricted to a zone close to the shore, and that their abundance (up to 212/m^2) stems from the lack of predators. Field observations over the past few years have shown that these beliefs are unfounded. Long-term ecological studies of 2 carefully mapped populations in the Bahamas have been initiated in an attempt to generate some basic information. The activities of over 900 individually marked animals have been followed periodically since November 1973. Recapture rates after the first 6 months were 70-80%. At that time half the snails were still within 1.0 m of their original positions and maximum displacement detected was 12.2 m. Information is also being gathered on predation, mortality and growth rates.

[1]This study was supported (in part) by research grant GB 35235 from the National Science Foundation, Washington, D.C., and by grants from the Clark and Milton Funds, Harvard University.

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NEWS AND ANNOUNCEMENTS

PUBLICATIONS ON NORTH AMERICAN FRESHWATER CLAMS. — Revised editions (with supplements) of *Freshwater sphaeriacean clams (Mollusca: Pelecypoda) of North America*, 96 pages, US$ 10.00, and *Freshwater unionacean clams (Mollusca: Pelecypoda) of North America*, approx. 200 pages, US$ 16.00, both by J. B. Burch, are now available. The 1st editions, now out of print, were prepared for the U.S. Environmental Protection Agency and printed by the Government Printing Office, Washington, D.C. The new editions can be purchased from Malacological Publications, P.O. Box 193, Hamburg, Michigan 48139, U.S.A. These publications contain illustrated taxonomic keys for the 39 species of North American bivalved mollusks of the superfamily Sphaeriacea (freshwater fingernail clams, pill clams, pea clams and nut clams) and for 227 species of the superfamily Unionacea (freshwater mussels). These common and widespread mollusks are often abundant in benthic samples from rivers, creeks, springs, ponds and lakes. North American species of Sphaeriacea belong to the genera *Sphaerium*, *Musculium*, *Pisidium* and *Eupera;* the Unionacea contain 46 genera in North America, including the well-known *Amblema*, *Anodonta*, *Elliptio*, *Fusconaia* and *Lampsilis*. Included in each of the publications is information on distribution, a synonymy, a bibliography, and for the Sphaeriacea, information on habitats.

AMERICAN MALACOLOGISTS, 1975 SUPPLEMENT. — A supplement for 1975 is now being prepared and will be ready for mailing in early spring. The cost will be US$ 1.00, and it will contain address changes and a listing of the names, addresses and interests of new registrants. A special discount of 20% is now offered on the purchase of the 1974 hardbound, 494-page volume to those who send in for a free application form. The new reduced price is US$ 10.00, plus 50 cents for postage and handling.

The managing editorship and main office of the national register of amateur and professional malacologists have now been entirely transferred to Dr. R. Tucker Abbott, P.O. Box 4208, Greenville, Delaware 19807. All correspondence, listings and orders should be sent to the new address.

BULLETIN OF THE MALACOLOGICAL SOCIETY OF CHINA, A NEW MALACOLOGICAL JOURNAL. — In August, 1974, the Malacological Society of China published the 1st volume of their new journal. Their *Bulletin of the Malacological Society of China* will henceforth be published yearly, with the aim of promoting interest and research on mollusks. Papers are published in either Chinese or English. The *Bulletin* may be purchased for US$ 5.00. All correspondence should be addressed to The Malacological Society of China, Taiwan Museum, Taipei, Taiwan, Republic of China.

Contents of the *Bulletin of the Malacological Society of China*, Vol. 1 (1974), are given on p 146 of this issue of *Malacological Review*.

ELONA, BULLETIN DE LIAISON DE MALACOLOGIE CONTINENTALE FONDAMENTALE ET APPLIQUEE. — *Elona* is a newsletter of basic and applied Continental malacology (especially on Recent and Quaternary land and freshwater mollusks of France), which succeeds the circulars of the Commission Faunistique Continentale of the Société Française de Malacologie. The original aim of this Commission was to study and apply mapping methods for an inventory of the Recent Continental mollusks of France. But, during the meetings of the Commission and through the circulars sent to its members, interests were broadened to include the method of labelling ecological data (e.g., in regard to biotope, to the species considered, etc.), establishing an inventory of reference collections, coordination with the European Invertebrate Survey for the mapping of European invertebrates, etc. It also became evident that the work and the data of the Commission Faunistique Continentale could interest many local as well as distant colleagues in fields other than Recent taxonomy and biogeography, e.g., ecologists, physiologists, parasitologists, applied malacologists, paleontologists, etc.

It is hoped that *Elona* will advertise individual and group interests and facilitate fruitful exchanges between malacologists and other specialists. The newsletter will appear once a year, scheduled generally in June. It will be distributed free to all members of the Société Française de Malacologie and to non-members on request for Fr. 5 per issue (paid to the order of Société Française de Malacologie - Commission Faunistique Continentale). For further information contact H. Chevallier, Muséum National d'Histoire naturelle, 55 rue de Buffon, 75005 Paris, France.

SUPPLEMENT 1, *MALACOLOGICAL REVIEW*. — "FRESHWATER SNAILS OF TAIWAN (FORMOSA)", by Gary L. Pace, 1973. This illustrated publication deals with the systematics, ecology, distribution, zoogeography and parasitological relationships of the freshwater gastropod fauna of Taiwan, The Republic of China. The price of this monograph (US $ 15.00 postpaid) is not included in the regular subscription price to *Malacological Review*, but can be purchased upon order from our American, Australian or Japanese editorial offices (see inside back cover for addresses).

CENTRO RICERCHE MALACOLOGICHE DI COPANELLO. — The Malacology Centre of Copanello is a private institution established to: (1) give practical training courses for underwater researchers and scholars; (2) give lectures and organize conferences on malacology; (3) organize expeditions for scientific study of marine shells; (4) undertake research enterprises to preserve underwater environments; (5) issue an annual bulletin about its research work. The Copanello Centre gives researchers full assistance, putting at their disposal boats and equipment (dredges and core barrels and underwater cameras, as well as a malacological laboratory, a library and a museum). The Centre gives lectures on malacology and the underwater world illustrated with slides, gives practical courses about marine shells found in the sea around Copanello, and organizes annual scientific expeditions abroad to study exotic shells. For further information write to the Director, Mr. Libero Gatti, Motel Copanello, 88060 Staletti, Catanzaro, Italy.

ANNOUNCEMENT OF SERVICES OF THE DEPARTMENT OF MALACOLOGY, ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA. — There are currently 336,000 cataloged lots of shells (about 10 million specimens) and 10,000 cataloged lots of alcohol-preserved mollusk material housed in the Academy of Natural Sciences of Philadelphia. The Academy's mollusk collection, one of the largest in the world, is especially outstanding in the following categories: Indo-Pacific and tropical western Atlantic marine mollusks, world land snails and freshwater mollusks, and chitons. Much of the material is historically quite important, including the 11,000 primary types.

As a result of financial support of the National Science Foundation, the Academy staff has finished general curation and updating of the marine gastropods and bivalves and the freshwater gastropods, and has nearly finished curating the Unionidae. The land snail collection is nearly ready for curatorial updating, i.e., 90% of the lots have been cleaned and numbered, with trays and vials replaced where needed. Cataloging an estimated backlog of 2500 lots of alcohol-preserved material has been started. Outside experts have been brought in to help curate various groups, such as minute marine gastropods, thecosomatous pteropods, Muricacea, Cerithiacea, Conidae, marine Rissoacea, Physidae, Helicinidae, Ampullariidae and Unionidae.

The Academy is currently inviting greater use of its mollusk collections. The Department of Malacology has a rapid and efficient loan service for qualified investigators wishing to borrow specimens for study, and will photograph specimens and photocopy literature for researchers. Alcohol-preserved specimens can be provided for anatomical studies of numerous taxa, researchers will be given information on distributions of species, and aid will be given in the identification of species. Technical assistance will be provided for visiting scientists who work with the collections. Also, the Academy will accept and preserve voucher specimens supporting ecological, physiological and biochemical research. — GEORGE M. DAVIS, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103, U.S.A.

VOUCHER SPECIMENS. — The American Council of Systematic Malacologists has formulated a policy to recommend to all scientific journal editors that voucher specimens of species used in all types of research papers on mollusks be lodged with a recognized repository. It is hoped that all scientific journals, whether specializing in mollusks or not, will follow this suggestion. This means that when a researcher publishes a paper on physiology, cytology, applied ecology or any other aspect of malacology, it is hoped that a condition of the journal's acceptance of the paper is that sample specimens of each species studied will be sent to a museum and that the registered numbers and full data of these specimens will be published. This will enable future workers to have easy access to this material, and it will also insure the accuracy of species determinations.

GYRAULUS WANTED FOR RESEARCH. — Dr. Claus Meier-Brook, Tropenmedizinisches Institut der Universität, 74 Tübingen, Wilhelmstrasse 11, Germany (FR) has requested preserved specimens in alcohol of the genus *Gyraulus* (Gastropoda: Basommatophora: Planorbidae) from Asia and Indonesia, and particularly mainland China.

SUMMER MALACOLOGY COURSE OFFERED BY TEXAS A & M UNIVERSITY. – The Department of Marine Sciences of the Moody College of Marine Sciences and Maritime Resources, Texas Agriculture and Mechanics University, will offer a course open to graduate students only entitled "Biology of the Mollusca" by S. M. Ray and W. J. Wardle during the second summer session, July 11 - August 15, 1975. Registration will take place on July 10, 1975. For further information write to: Head, Department of Marine Sciences, Moody College of Marine Sciences and Maritime Resources, Bldg. 311, Fort Crockett, Galveston, Texas 77550, U.S.A.

DUCK RIVER CASE DECIDED. – Environmentalists and conservationists should be pleased to learn that the court case (see *Malacol. Rev.*, 1974, 7: 62) to halt construction of two Tennessee Valley Authority (TVA) dams on the Duck River in Tennessee has been decided in favor of preserving the rivers. Entering prominently into the case was the effect the dams would have on the freshwater mollusk fauna of the river.

The Duck River, which flows through an unusually beautiful and ecologically diverse region, is the longest remaining wild river in Tennessee. Most of the other major streams, once supporting one of the richest molluscan faunas in the world, have been badly impounded by the many TVA dams in the region. The Duck River Preservation Association and the Environmental Defense Fund contended that the TVA project would inundate wildlife habitats, archaeological and historic sites, would remove 41,000 acres of prime agricultural land from production, would threaten extinction to certain animal species, and would displace about 400 families. David H. Stansbery testified as to the adverse effect the TVA dams would have on the freshwater mollusks, and Curtis Bohlen, Deputy Assistant Secretary of the U. S. Department of the Interior, recommended that construction of the dams be halted to prevent serious threats to the continued existence of several species of clams in the Duck River. TVA attempted to counter these assertions and recommendations about the mollusks with the testimony of Henry van der Schalie.

Charging that TVA suppressed important information about its Duck River project, U. S. District Judge Charles G. Neese issued an injunction to stop construction of the dams. Information concerning estimated farm losses and relocation costs was omitted from TVA's environmental impact statement for the project, although such information had been collected and prepared by TVA's own economists for inclusion in the statement. At the trial held in Winchester, Tennessee, it was revealed that 4.6 million dollars would be lost annually by farm-dependent businesses and that if all agricultural losses had been considered by TVA, the annual cost of the project would outweigh the projected benefits. TVA's impact statement claimed that losses from reduced agricultural production would be "offset many times over by the economic gains that will result from this project." Claiming that the injunction ordered by the Court would be costly and would put many construction people out of work, TVA requested a stay of the injunction until June 30, 1974. Judge Neese granted TVA's motion, but stated that "it was not this Court that put men out of work, it was TVA's violation of the law." [Some of the above was excerpted from *EDF Letter*, a publication of the Environmental Defense Fund.]

SOCIETIES' NEWS

* * *

A BRIEF HISTORY OF THE MALACOLOGICAL SOCIETY OF AUSTRALIA: 1953-1973. — Following private meetings in late 1952 of a small number of Melbourne people interested in shells, The Malacological Club of Victoria held its 1st public meeting in January, 1953. Meetings were held at the National Museum of Victoria with Mr. John Crofts as the first President, Mrs. Thelma Hartley as Secretary, and Miss J. H. MacPherson, Conchologist at the Museum, as Patroness. At the end of the 1st year, there were 46 members. In the next few years membership increased to 120, the Rev. John Arnold became President and upon the death of the latter, was succeeded by Mr. Denzil Hartley. Meetings were held at the Auction Room, Scott's Hotel (now demolished) and then at the lecture room of the Royal Society of Victoria. Mr. Hartley remained as President until his death in 1964. Except for 2 brief absences, Mrs. Thelma Hartley was Secretary/Treasurer of the Society from its inception in 1953 to her husband's death in 1964. Upon her retirement from this position, honorary life membership was conferred upon Mrs. Hartley.

In 1957 the name of the Society became the Malacological Society of Australia. Growth of membership led to the formation of branches at various centres where sufficient numbers resided. The Sydney Branch was formed in 1961 under the leadership of Dr. D. F. McMichael. Other branches were formed at Brisbane and Proserpine in 1963, and at Taree, Townsville and Port Moresby in 1966. Of these, Sydney, Brisbane and the Victorian Branches are still active and hold regular meetings. There are now nearly 500 members of the Society. Of those who joined the Society in its 1st year and have maintained continuous membership for the full 20 years of its existence, there remain 4 members. These are Mrs. Thelma Henry of Florida, U.S.A. (formerly Mrs. D. I. Hartley of Melbourne), Mr. Robert Burn of Victoria, Mr. F. S. Colliver of Queensland and Dr. B. R. Wilson of Western Australia.

Administration of the Society until 1964 was a function of the committee of the Victorian Branch. Upon Mr. Hartley's death in December of that year and Mrs. Hartley's resignation from the position of Secretary/Treasurer, administration of the Society passed to the Sydney Branch. Reorganization of affairs in 1965 led to the separation of Society and Branch business, with a Council under the guidance of Mr. T. A. Garrard as President in charge of Society matters, and a Sydney Branch with its own executive. Dr. D. F. McMichael became President in 1968 and held this position until administration of the Society was transferred to Melbourne in 1972.

Publications of the Society have enhanced its reputation, and have been a boon to both members and non-members. A quarterly "Australian Newsletter" has been published regularly since April, 1953. Sixty issues were published in roneoed (mimeographed) form, followed by 20 issues to 1973 in offset printed form with figures and photographs. In January, 1973, the title was changed to "Australian Shell News."

Scientific publications, useful to both the amateur and professional, commenced with "Publication No. 1: Family Thaididae," a 4 page illustrated folder for the identification of Australian species of this family. This was followed by "No. 2: Family Littorinidae," October, 1956, "No. 3: Family Turritellidae," March, 1957, and "No. 4: Family Cymatiidae," April, 1957. These were prepared by the late Bernard C. Cotton, then Conchologist of the South Australian Museum. Since November, 1957, the Society has annually published the *Journal of the Malacological Society of Australia*. Volume 1 appeared in 12 parts between 1957 and 1969, and was available to subscribers only. Volume 2, published between 1970 and 1973, became one of the benefits of membership of the Society and was received by all members. The *J. malacol. Soc. Austr.* was edited from 1957 to 1959 by Mrs. T. Hartley, in 1960 by the late Miss F. Murray, from 1961 to 1968 by Dr. D. F. McMichael, and since 1969 by Mr. R. Burn. Articles written by many members have been published over the years, as well as many by leading overseas and Australian malacologists. — ROBERT BURN

SOCIETÀ MALACOLOGICA ITALIANA. — The Italian Malacological Society is a centre for the study of continental, marine and fossil mollusks. The Society's aims are: to increase the malacological studies concerning chiefly the Italian fauna; to favour the relationship between scholars and others interested in malacology; to represent the Italian malacologists in the "Unitas Malacologica Europaea" and in other malacological societies.

Research fields. Italian malacologists investigate mollusks from the point of view of evolution, systematics, physiology, ecology, biogeography, etc. Excursions, lectures and lessons are also included among the activities of the Society. The Italian Malacological Society cooperates with investigators in other scientific areas, such as limnology, human and veterinary parasitology, paleontology and archeology. Members have at their disposal a library as well as bibliographic data of the library holdings of many scholars and joint institutes. This is a necessary service to start malacological research. The Society does not permit gathering shells with the sole aim of making collections.

Activities. 1964 - The 1st volume of *Lavori della Società Malacologica Italiana* is a collection of the most important papers of the members; 1965 - The publication of *Schede Malacologiche del Mediterraneo* began; 1966 - The 1st Italian Meeting of Malacology (Pallanza); 1969 - Symposium on "Ecological problems of freshwater Mollusca" (Milano); Symposium on "Importance of Mollusca in pollution problems" (Ispra); 1970 - 2nd Italian Meeting of Malacology (Genova); International Symposium of "Ecology of Mediterranean Mollusca" (Genova); 1971 - Italo-French Symposium of "Mollusca of Alps" (Lyon); 1972 - Symposium on "Tertiary and Quaternary malacofauna. Their paleoecology and paleobiogeography" (Verona); 1973 - Meeting at Varenna with the German Malacological Society; Symposium on the "Penetration of recent Mollusca in the Mediterranean Sea" (Milano); 1974 - Organisation of the 5th Congress of Unitas Malacologica Europaea (Milano); International Meeting on Polymorphism of Gasteropods (Milano).

Application. All persons and institutes interested in or devoted to the study of mollusks can become members of the Italian Malacological Society. The Society does not accept the application of shell collectors and supports all measures to prevent the destruction of mollusks for profit. The application enquiry should be sent to: Segreteria della Società Malacologica Italiana, Corso Venezia, 55, 20121 - Milano, Italy. It should include the name, surname, research institute, address and prevalent field of interest or research, and it must be cosigned by 2 members of the Society. — A. GIROD

MALACOLOGICAL SOCIETY OF CHINA. — In 1968, the 3rd specimen of *Pleurotomaria rumphii* Schepman was discovered off Taiwan and was subsequently purchased by a museum in Japan for US$ 10,000. The extremely high price commanded by this specimen aroused a great deal of enthusiasm among the public and raised their interests for precious shells as well as malacology in general. The first shell exhibition to take place in Taiwan was held in 1969 at the Taiwan Museum, attracting more than 30,000 visitors during the ten-day period. In this exhibition, more than 7,000 specimens were shown, including some fossils. The following themes were represented: Systematics and Evolution, Mollusks and Civilization, Shellcrafts, Mollusks and Medicine. Three additional exhibitions were held in the following years, twice in Taipei and once in Kaohsiung.

The Malacological Society was founded in October 1970 after meetings of some 30 promoters. It has more than 200 active members at present, with about a dozen foreign members. The membership is open to all individuals interested in the field of malacology. Dues are US$ 4.00 per year for individuals and US$ 8.00 for institutions. The Society publishes the *Bulletin of the Malacological Society of China*, with one issue per year currently scheduled. The 1st issue (Vol. 1) was published in August, 1974. It has 150 pages, contains 15 articles and 15 other items such as news, announcements, membership directory, bibliography on mollusks of Taiwan, etc. Volume 1 can be obtained from the Society by sending US$ 5.00. A few complimentary copies are still available on request. The *Bulletin* welcomes papers written in Chinese or English, with summaries in the reciprocal language. Inquiries should be addressed to: Malacological Society of China, c/o Taiwan Museum, Taipei, Taiwan 100, Republic of China. — C. T. LO

SOCIÉTÉ BELGE DE MALACOLOGIE. — Activities during the year will include the following discussions: January 25, 1975 - Family Cypraeidae (continued), subfamily Erroneinae, genera *Ovatipsa* (*chinensis*, *coloba*, *caurica*), *Talostolida* (*teres*, *rashleigniana*, *latior*, *subteres*, *goodalli*) and *Bistolida* (*stolida*, *brevidentata*, *erythraeensis*), by J. BUYLE; February 8, 1975 - Genus *Tibia*, by M. LAMBIOTTE; February 22, 1975 - Family Cypraeidae (continued), subfamily Erroneinae (continued), genus *Blasicrura* (*pallidula*, *interrupta*, *luchuana*, *summersi*, *quadrimaculata*, *coxeni*) and subfamily Talpariinae, genera *Talparia* (*talpa*, *exusta*), *Basilitrona* (*isabella*, *isabellamexicana*, *pulchra*) and *Luria* (*lurida*, *cinerea*), by J. BUYLE; March, 8, 1975 - Thailand and marine benthic fauna of the Western coast with projection of slides, by J. SENDERS; March 22, 1975 - Family Cypraeidae (continued), subfamily Talpariinae (continued), genera *Chelycypraea* (*testudinaria*), *Arestorides* (*argus*) and *Macrocypraea* (*zebra*, *cervus*, *cervinetta*), subfamily Austrocypraeinae, genus *Austrocypraea* (*reevei*), subfamily Cypraeovulinae, genera *Cypraeovula* (*capensis*, *amphithales*) and *Luponia* (*algoensis*, *edentula*, *cohenae*, *fuscorubra*, *gondwanalandensis*, *fuscodentata*), by J. BUYLE. Inquiries should be sent to the Société belge de Malacologie, Avenue des Lilas 54, 1410 Waterloo, Belgium.

During 1974, the following articles appeared in the Society's *Informations de la Société Belge de Malacologie:* J. CHRISTIAENS, Les Fissurelles européennes, III. Le genre *Diodora* Gray, 1821, *sensu* Iredale, 1915 - Les *Diodora* européennes - Espèces non-européennes; J. CHRISTIAENS, Additifs à la "Revision du genre *Patella*"; R. DUCHAMPS, Les marées de 1974 (2); W. FASSEAUX, Sur quelques microcoquilles européennes: quelques considérations sur les Acteoninae; W. FASSEAUX, *Chrysallida sarsii* Nordsieck, une nouvelle espèce sur la côte belge; E. FISCHER-PIETTE, Sur l'aire de distribution de *Pitar* (*Lamelliconcha*) *madecassina* Fischer-Piette et Delmas; A. V. GROSSU and C. TESIO, Etudes électrophorétiques pour la confirmation du genre *Herilla* H. et A. Adams (Clausiliidae); A. KERMARREC-LABISSE, Présence en Martinique de *Melongena melongena* (Linné, 1758); H. K. MIENIS, Notes on molluscs from Cyprus, 1: the genus *Levantina;* H. K. MIENIS, Reports on Neritidae, 1: Notes on a small collection from Kenya; H. K. MIENIS, A checklist of Strombidae from the Sinai-area of the Red Sea; R. A. VAN BELLE, A propos du genre *Ischnochiton* Gray, 1847 (Polyplacophora).

MOLLUSK SEMINAR, ANN ARBOR, MICHIGAN, JUNE 1974. — A seminar on mollusks was held at The University of Michigan, Ann Arbor, on 22 June 1974. The papers presented at the seminar are listed below.

Scanning electron microscope studies of the shell apices of freshwater limpets. J. B. BURCH
Scanning electron microscope study of radular teeth of *Physa gyrina hildrethiana* (Basommatophora: Physidae). George A. TE and A. John MARDINLY
Current taxonomic studies on the family Physidae. George A. TE
How fast is a snail's pace? Active and passive dispersal of *Physa integra* in Douglas Lake, Michigan. Philip T. CLAMPITT
Snail host-specificity of the nonhuman schistosome, *Gigantobilharzia huronensis* Najim 1950. Harold J. SAUER, Bernard GONIK and Harvey D. BLANKESPOOR
Studies on the food and feeding habits of European snails. June CHATFIELD
Cultivating *Fossaria bulimoides* (Lea), a snail host of the liver fluke, *Fasciola hepatica*. Yung-san LIANG and Henry VAN DER SCHALIE
Some observations on gastrulation of the gastropod *Ilyanassa*. Michael CRAIG
DDT in terrestrial slugs. Karl-Hans WURZINGER
Electrophoresis of *Stagnicola elodes* hemolymph. Paul H. RUDOLPH
Esterase patterns of some diploid *Bulinus* populations. Gene K. LINDSAY and J. B. BURCH
Systematic studies on the genus *Bulinus* from Algeria. Philip T. LoVERDE, Kamel ADDADI and J. B. BURCH
A new approach to the systematics and ecology of the genus *Cerion*. David S. WOODRUFF

UNITAS MALACOLOGICA EUROPAEA, FIFTH EUROPEAN MALACOLOGICAL CONGRESS. — The 5th European Malacological Congress was held in Milan, Italy, from 3-7 September 1974. It was preceded by a Symposium on Polymorphism of Gastropods which was held on 2 September. The papers or abstracts will be published in *Malacologia*. The papers presented are listed below.

Symposium on Polymorphism of Gastropods

J. GAILLARD, Le polymorphisme de *Littorina saxatilis*.
A. GROSSU, Le polymorphisme des gastéropodes et la possibilité d'identifier et limiter l'espèce avec les méthodes biochimiques.
D. LUPU, Le polymorphisme chez quelques espèces appartenant aux familles Limacidae et Arionidae (Gastropoda - Pulmonata) de Roumanie.
J. C. PLAZIAT, Les Cérithidés tropicaux et leur polymorphisme lié à l'écologie littorale.
E. BINDER, Le Polymorphisme de la coloration de la coquille chez *Pachymelania aurita* (Müller).
C. F. SACCHI, La variabilité de *Littorina saxatilis* (Olivi) et l'identité specifique de *L. nigrolineata* (Gray) (Gastropoda, Prosobranchia).

Fifth European Malacological Congress

F. TOFFOLETTO, etc., Welcoming remarks.
W. BACKHUYS, Zoogeographical and taxonomical research in Macaronesia, especially the Azores.
E. GITTENBERGER, Die Einteilung der Chondrinidae (Pupillacea).
L. PINTÉR, Über das System der Helicidae *sensu lato*.
F. STARMÜHLNER, The genus *Paludomus* in Ceylon.
C. M. YONGE, Evolution within the Pectinacea.
J. CHATFIELD, Preliminary studies on the distribution of the land snail genus *Monacha* in western Europe.
A. C. VAN BRUGGEN, A preliminary analysis of African non-marine Gastropoda Euthyneura families.
A. MEAD, The giant African snail *Achatina fulica* and economic malacology.
E. ÄNT, Land- und Süsswassermollusken als ökologische Zeigerarten.
L. ERDÉLYI, Synaptic activation of *Helix* ganglion cells by barium ions.
M. L. SILVA SAMPAIO (XAVIER), V. F. SIMON, A. I. CONCEICAO and M. V. RAMAJO, Susceptibility of *Planorbis metidjensis* from Portugal and Salamanca (Spain) to the strain of *Schistosoma bovis* from Salamanca.
M. DERER, Ultrastructure de l'organe de perforation de *Thais lapillus* (Gastropode - Prosobranche).
J. VOVELLE, M. GRASSET and F. MEUNIER, Elaboration de l'opercule calcifié chez *Nerita plicata* L. et *Pomatias elegans* (M.), Gastéropodes Prosobranches.
R. VAN COILLIE, A. ROUSSEAU and G. VAN COILLIE, Cycles physiologique et biologique saisonniers chez un gastéropode d'eau douce.
A. GIROD, Les Mollusques du lac de Lugano.
M. MARIANI and O. RAVERA, Quantitative and qualitative differences among some mollusc populations in two basins of the lake of Lugano.
C. MEIER-BROOK and Kim CHONG-HWAN, Notes on ciliary feeding in two Korean *Bithynia* species.
A. D. ANSELL, Bivalve ecology.
V. YOLOYE, The biology of *Iphigenia truncata* (Bivalvia Tellinacea).

J. WAUTIER, Preliminary data on the geographical range of the freshwater limpet *Ferrissia wautieri*.
V. YOLOYE and O. S. ADEGOKE, A new species of *Neritina* (Archaeogastropoda, Neritidae) from the Lagos lagoon.
J. H. JUNGBLUTH, Some species of *Bythinella* in Central Europe (Prosobranchia, Hydrobiidae).
F. GIUSTI and E. PEZZOLI, The genus *Bythinella* in Italy.
C. THIRIOT-QUIEVREUX, Identification des larves planctoniques de gastéropodes.
F. X. NEIL, L'alimentation d'*Aplisia punctata* Cuvier de la Ria de Vigo.
C. F. SACCHI, A. M. TORELLI and D. VOLTOLINA, L'alimentation de *Littorina saxatilis* (Olivi) dans la lagune de Venise.
M. KERNEY, Mapping the land and fresh-water Mollusca of Europe.
H. CHEVALLIER, H. ANT and M. KERNEY, National or local projects.
J. HEATH, The progress of the European invertebrate survey.
E. KROLOPP, Angaben zur Entfaltung der mitteleuropäischen fluviatilen Molluskenfauna.
P. E. P. NORTON, Neogene Mollusca of Tjörnes, Iceland.
A. SOLEM and E. S. RICHARDSON, Structure and affinities of a paleozoic radula.
S. HADŽIŠČE and J. B. BURCH, The systematic position of *Gocea ohridana*.
J. A. SNELI, The marine Mollusca of Jan Mayen.
P. PANETTA, Les "Citri" de la "Mar Piccolo" de Tarante.
H. H. BOER, Structure and function of the heart-kidney system of some gastropods.
R. ROBERTSON, Biological systematics and ecology of east American *Odostomia* (Pyramidellidae).
P. F. NEWELL and A. C. BROWN, The fine structure of the osphradium of *Bullia* (Gastropoda, Prosobranchiata).
N. W. RUNHAM, Studies of the effects of castration in the pulmonate *Agriolimax reticulata*.
M. RICHARDOT, Mitochondria and intracellular calcification in *Ferrissia wautieri* (Gastéropode Ancylide).
J. B. BURCH, S. HADŽIŠČE and C. M. PATTERSON, Studies on Lake Ohrid pulmonate mollusks.
P. BOUCHET, The molluscan fauna of the west African mangroves: a comparison with other mangroves.
B. S. MORTON, The population dynamics of *Limnoperna fortunei* in Plover Cove reservoir, Hong Kong.
C. GROSSO and O. RAVERA, Population dynamics of *Viviparus ater* from the Lake of Lugano.
O. RAVERA, Effects of heavy metals on a freshwater snail: *Biomphalaria glabrata* (Gastropoda, Pulmonata).
T. SMINIA, Structure and function of blood and connective tissue cells of the basommatophoran snail *Lymnaea stagnalis*.
T. A. DE VLIEGER, A survey of the neurophysiology of *Lymnaea stagnalis*.
J. JOOSSE, A survey of the data on the endocrinology of *Lymnaea stagnalis*.
W. J. VAN DER STEEN, Effects of crowding in freshwater snails: reality or myth?
K. BÁBA, Die kontinentalen Schneckenzönosen der Eichen-Ulmen-Eschen-Au-Wälder, *Fraxino pannonicae-Ulmetum pannonicum* Soò/ der Ungarischen Tiefebene/Alföld/.
P. F. NEWELL, The structure and enzyme-histochemistry of slug skin.
T. GASCOIGNE, Sacoglossan teeth.
G. POSSI and M. MERLINI, Radiozinc accumulation by the prosobranch gastropod *Viviparus ater* (Cristofori and Jan).
M. J. BISHOP, An approach to the quantitative description of terrestrial mollusc associations and habitats.
F. GHISOTTI, Specific and generic identification in malacology through perforated cards.
F. GIUSTI, A malacological survey of Sardinia.
A. WIKTOR, Zur Verbreitung der Nacktschnecken, Arionidae, Milacidae, Limacidae - Pulmonata, Gastropoda/ in Bulgarien.
A. VAN GOETHEM, La systematique des Urocyclinae (Mollusca, Pulmonata, Urocyclidae).
O. SCARLATO, Distribution of bivalve mollusks.

MEETING OF THE INSTITUTE OF MALACOLOGY. — A meeting of the Institute of Malacology was held at the Academy of Natural Sciences, Philadelphia, on December 19, 1974, presided over by the President, Dr. Robert Robertson. Other members attending were J. B. Burch (President-Elect), M. R. Carriker, G. M. Davis (Executive Secretary-Treasurer), C. F. E. Roper and S. K. Wu. The main business discussed was the affairs of *Malacologia*. Elected to alternate Sponsor Membership in the Institute of Malacology were R. D. Turner and W. D. Russell-Hunter. Future annual meetings of the Institute of Malacology will be held at a convenient place as decided by the Sponsor Members. One Member-at-Large (i.e., any subscriber to *Malacologia*) may attend and vote at the annual meeting by petitioning the Institute of Malacology in advance. Inquiries should be directed to the President.

SYMPOSIUM BY THE GRUPPO NATURALISTICO MANTOVANO "LUIGI D'ARCO" AND THE SOCIETÀ MALACOLOGICA ITALIANA. — The Mantuan Naturalistic Group and the Italian Malacological Society have organized a national symposium to be held in Mantua, Italy, on May 10 and 11, 1975. There will be no restriction on the subjects to be discussed, but particular attention will be paid to the malacofauna of Northern

Italy. On the same occasion, an ancient nature book exhibition, chiefly concerning malacological works, will be held in the Sala Teresiana of Mantua's town library. Inquiries should be sent to Dario A. Franchini, 1st Symposium sui Molluschi, 37 Via Cremona, I-46100, Mantova, Italy. — D. A. FRANCHINI

SOCIÉTÉ FRANÇAISE DE MALACOLOGIE. — The French Malacological Society will hold 2 meetings during 1975. The 1st will be a symposium on Polymorphism in Fossil and Recent Molluscs to be held in Dijon (Institut des Sciences de la Terre de l'Université de Dijon, France) on 7 and 8 March 1975. The 2nd meeting will be the Third Congress of the French Malacological Society, to be held in La Rochelle (Institut Universitaire et Technique de La Rochelle, France) on 16-22 June 1975. During this Congress an international symposium will be held on Applied Marine Malacology. Authors of communications must be members of the Society. For further information write to the Société Francaise de Malacologie, 55 rue Buffon, 75005 Paris, France. — H. CHEVALLIER

JOINT MEETING OF THE AMERICAN MALACOLOGICAL UNION AND THE WESTERN SOCIETY OF MALACOLOGISTS. — The 41st annual meeting of the American Malacological Union and the 8th annual meeting of the Western Society of Malacologists will be held jointly on June 22-26, 1975, at San Diego State University, San Diego, California. The program will include contributed papers, symposia, exhibits, and study workshops on various molluscan subjects. Inquiries about the meeting should be directed to Clifton Martin, Secretary (WSM), 324 Kennedy Lane, Oceanside, California 92054, or to Donald R. Moore, School of Marine Science, University of Miami, 10 Rickenbacher Causeway, Miami, Florida 33149.

Applications for membership in the American Malacological Union should be sent to Paul R. Jennewein, Corresponding Secretary, P.O. Box 394, Wrightsville Beach, North Carolina 28480. Applications for membership in the Western Society of Malacologists should be sent to Bertram C. Draper, Treasurer, 8511 Bleriot Avenue, Los Angeles, California 90045. — G. E. RADWIN and P. R. JENNEWEIN

BOOKS

AMERICAN SEASHELLS. Second Edition. R. Tucker Abbott. Van Nostrand Reinhold, 450 West 33rd Street, New York, N. Y. 10001, U.S.A. 1974. 663 p, 6405 figs., 24 pls. US $ 49.50.

Updated and almost doubled in size, this is the second edition of Dr. Abbott's well-known American Seashells published in 1954. With the current edition, all 6,500 known species of marine mollusks living in the waters adjacent to North America are listed for the first time, and over 3,000 of them are illustrated and described in detail. The index contains over 14,000 entries. There are more than 4,000 black-and-white illustrations and 24 color plates. From the geographical distributions and bathymetric ranges given for each species, collectors may predict what kinds of shells they are likely to find from Quebec to Texas or from Alaska to the Gulf of California. Because of the identification keys, the updated nomenclature, and ecological and geographical information, the volume will be invaluable to the professional malacologist. This edition is considerably upgraded in technical treatment, and is now an even more useful research tool in shellfishery studies, anti-pollution investigations and marshland conservation projects. Besides its value to the research worker in marine mollusks, it will serve as source material for the marine geologist, the ecologist, the oceanographer, the zoologist, the taxonomist, and other scientists.

FAUNA OF THE ARMENIAN SSR. MOLLUSCA. [In Russian.] N. N. Akramowski. Publishing House of the Armenian Academy of Sciences. 1975. Estimated price 2 rubles, 30 kopeks.

The book contains descriptions of 153 species now inhabiting the territory of Soviet Armenia, with keys for identification. The volume begins with a general part. It comprises the following chapters: morphological introduction, an outline on ecology, molluscs as pests in agriculture and stock-raising, a brief survey of the control of injurious species, a geographical analysis of the fauna, instructions for faunal and taxonomic investigations.

The descriptions of 133 gastropod species (from a total of 141 species covered) are supplied with figures of the genital organs and other taxonomically important features. A hundred and nineteen of the figures are original drawings by the author. The figures of the genital systems of 20 species are published for the first time. Original figures of hinge-plates are given for all 12 bivalve species. Two hundred and seventy original photographs of slugs and shells of nearly all shell-possessing species are given in 16 plates. In some cases molluscs are illustrated in several positions.

The book is intended as a source of information to zoologists, and to malacologists in particular. It can also be used by specialists in contiguous fields dealing with mollusc studies such as helminthology, hydrobiology, pest control, terrestrial ecosystems and paleontology of the Neogene and Quaternary sediments.

Preliminary orders from foreign countries should be sent to local book-selling organizations having relations with the Soviet All-Union Alliance "Mezhdunarodnaia Kniga."

SEATTLE SHORELINE ENVIRONMENT. Randall McGreevy. Published by the City of Seattle Department of Community Development and the Washington Sea Grant Program, distributed by the University of Washington Press, Seattle, Washington 99195, U.S.A. 1974. 48 p, maps, photographs. US$ 1.95.

Seattle, with its great metropolitan population and inherent forces of urbanizations, has painfully imposed high and many times irreversible costs of arbitrary and irresponsible uses upon shoreline environments. The alterations have changed the character and nature of our shorelines . . . Seattle's altered shorelines are still ecologically abundant and diverse and will continue to be if sincere consideration is given to essential ecological requirements. This booklet is a description of the abundant resources of Seattle's natural shoreline and is dedicated toward a better identification and deeper appreciation of Seattle shoreline environment with an eye toward developing an informed government and citizenry. Maps and photographs as well as a descriptive analysis show the shoreline's natural phenomena, identify major alterations and locate resources. This volume is a supplement to the earlier Seattle Shoreline Inventory published by the Office of Environmental Management in compliance with the Washington State Shoreline Management Act of 1971. It should be of serious interest not only to aquatic biologists, but to all citizens.

Malacological Review, 1975, 8: 139-197

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THE AMERICAN MALACOLOGICAL UNION, Inc.

BULLETIN
for 1973

Published
May 22, 1974

AMU Thirty-Ninth Annual Meeting

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Most scientific journals send manuscripts to qualified reviewers to assist authors in avoiding errors and in improving their papers. The AMU has now adopted a similar policy. The AMU Council constitutes our review board and all manuscripts except abstracts are sent to appropriate members of this review board (usually two) prior to acceptance for publication.

The AMU Bulletin has also adopted as its standard the *Style Manual for Biological Journals* published by the American Institute of Biological Sciences, Washington. All manuscripts accepted for publication become the property of the AMU and may be edited for style in accordance with this standard.

The American Malacological Union, Inc.
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Pleurotomaria rumphii

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August, 1974

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1. 本誌刊登會員及非會員一切有關軟體動物之未經發表的文章，以及國內外貝類團體活動稿件。雖以中文爲主，但英文稿件亦甚歡迎。
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This Bulletin is published yearly by the *Malacological Society of China* for the promotion of interest and research in mollusks. Papers in Chinese or English are considered. Summaries in reciprocal language will be attached which may be prepared by the author or by the editorial staff. Interested persons are cordially invited to join the Society. Foreign membership fee is US$4.00 or its equivalent per year (postpaid) for individuals and US$8.00 for institutions. The Bulletin may also be obtained for US$5.00 to cover cost of printing. Please send manuscripts and all correspondence to: **The Malacological Society of China, Taiwan Museum, Taipei, Taiwan, China** (Tel. 313261, Taipei).

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爲加强與國外貝類團體之合作，本會曾致函各國之貝類學會查詢，結果下列各團體或雜誌已同意與本刊合作，互相交換出版物，並提供調查資料等之服務。有些學會表示限於會章規定，不便交換刊物，但本會仍擬贈送會誌。

BULLETIN OF THE MALACOLOGICAL SOCIETY OF CHINA is affiliated with the following organizations to an extent that there will be exchange of publications and information, and a limited degree of gathering information and answering questions for members of affiliated organizations.

- The Academy of Natural Sciences of Philadelphia
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中華民國貝類學會
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MONTEVIDEO - URUGUAY

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OF THE
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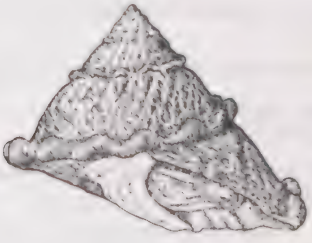

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(Cerithiidae: Prosobranchia)

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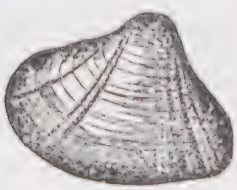

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Volume X

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Landgastropoden innerhalb einer Großstadt am Beispiel von Halle an der Saale

mit 1 Abbildung

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Helicellen von der Finne zwischen Bad Sulza und Eckartsberga

mit 1 Karte

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mit 5 Abbildungen

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mit 1 Karte

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mit 1 Figur

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Verbreitung der Weinbergschnecke Helix pomatia Linnaeus, 1758 im Leipziger Auewald

mit 8 Karten

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mit 2 Abbildungen

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mit 1 Karte

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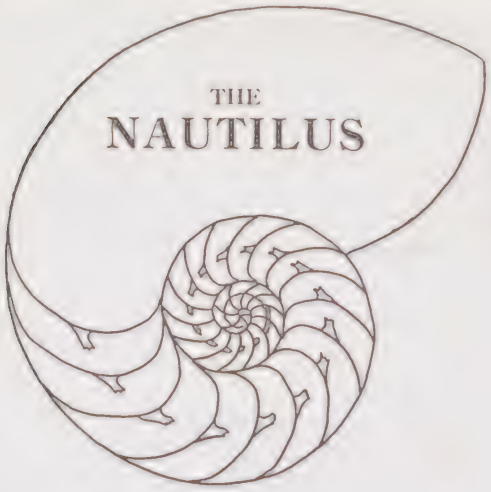

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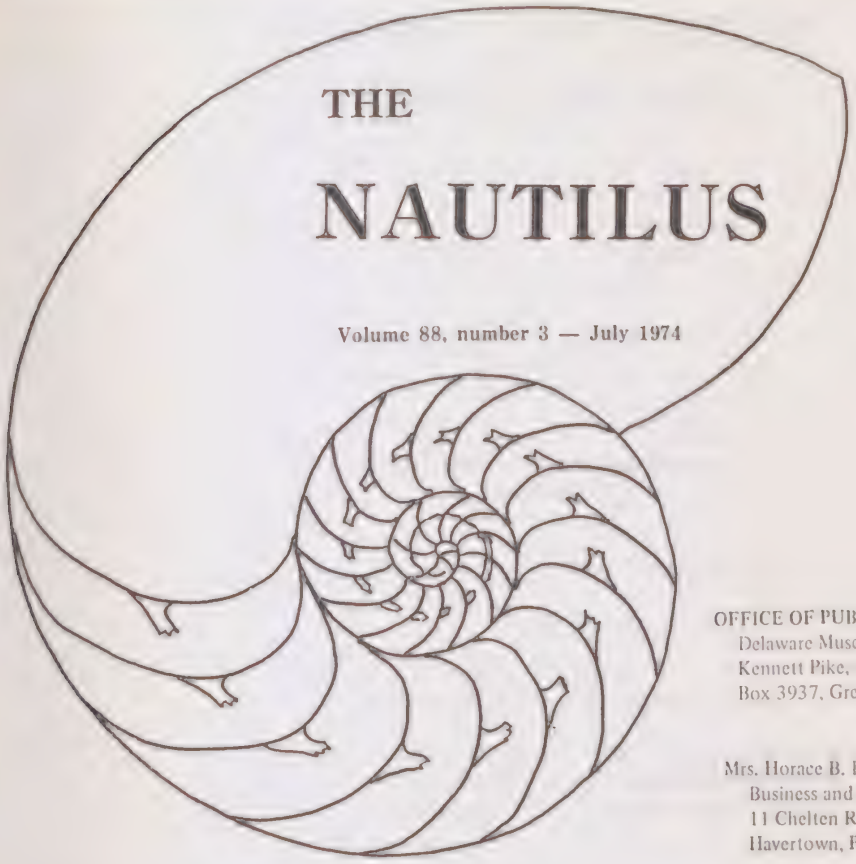

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Occasional Papers On Mollusks

PREFACE

During the last 30 years malacology has enjoyed increasing attention. In the Preface to Volume 1 of *Occasional Papers* it was stated that malacological literature in 1954 amounted to some 1000 articles in more than 200 journals and that the phylum contained an estimated 200,000 species. In the interim, both the estimate of the total number of living species of mollusks and the annual volume of published literature have changed. In a recent Zoological Record (vol. 107, 1974), which covers the literature for the year 1970, articles dealing with mollusks number over 2500, published in several hundred journals by over 1000 authors, representing more than a two-fold increase in twenty years.

The species concept in zoology, as currently understood, emerged from the synthesis of ideas in taxonomy, genetics and paleontology. The New Systematics, which recognizes that species are unique, dynamic, natural units consisting of interbreeding populations with characteristic genetic, physiological and morphological features, has made a reappraisal of the species-level diversity of mollusks necessary. Detailed reference to more recent and critical investigations lends credence to the contention that there are fewer than 50,000 living species (Boss. 1971. Occ. Papers Moll., Harvard Univ., 3: 81–135). In well studied groups, which have received careful taxonomic revision and monographic review, virtually every species has been named more than once and frequently several times. In highly variable organisms such as pearly-freshwater mussels, a few species have hundreds of synonyms.

Many molluscan species are still poorly known and there are yet more to be discovered in nature; however, it is disconcerting in the extreme to observe the haphazard, almost unrestrained flow of descriptions of new species. Almost each issue of such malacological journals as the *Archiv für Molluskenkunde*, *Venus*, and *The Veliger* contain newly introduced taxa. These descriptions are often parochial in scope and are not published in conjunction with thorough systematic revisions. Frequently they are obviously uncritical and biologically unsound, considering what is known about genetic variability of species and the attendant range of morphological variation. One questions the validity of a new *Limax* described from Austria when there are over 500 available nomina for Palearctic slugs (Hesse, P. 1929. Die Nacktschnecken der palaearktischen Region. Abhand. Arch. Moll. 2 (1): 152 pp.) or a new *Littorina* from Baja California when there are at least 1200 available names in that genus (Rosewater, J. 1970. The family Littorinidae in the Indo-Pacific. Indo-Pacific Mollusca, 2 (11): 417–506; *pers. comm.*)

Further, the proliferation of superspecific, i.e. generic, subgeneric and familial level nomina, is astonishing and obfuscates rather than elucidates evolutionary relationships. The student can hardly find a cowry which is referable to *Cypraea* or a muricid which can be placed in *Murex*. A perfectly recognizable volutid from Australia may be set in unfamiliar *Nannamoria* while a hydrobioid from the Balkans may be placed in one of 75, mostly monotypic, genera.

There is, in short, a vast nomenclatorial surplus in malacology which casts doubt on the validity of many of the new taxa still being introduced. We believe that the few new species which appear in this volume are critically described and that the several catalogues illustrating the taxa introduced by a number of authors will help to reduce the renaming of species in certain difficult groups.

K. J. Boss

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MONOGRAPH OF THE GENUS *LUCIDELLA* IN CUBA
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By KENNETH J. BOSS AND MORRIS K. JACOBSON

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GÖTTING, KLAUS-JÜRGEN. 1974. *Malakozoologie. Grundriss der Weichtierkunde.* Gustav Fischer, Stuttgart, X + 320 pp., 160 figs.
— K. J. BOSS

VOLUME 4 15 NOVEMBER 1974 NUMBER 49

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BY

HELEN DUSHANE

Research Associate
Los Angeles County Museum of Natural History
Los Angeles, California 90007

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Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor

BY

E. C. HADERLIE

Department of Oceanography, Naval Postgraduate School,
Monterey, California 93940

(44 Text figures)

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